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Effect of fuel load, date, rain and wind on departure decisions of a migratory passerine

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Abstract Meteorological conditions, fuel load and date in the season can affect the departure decisions among migratory birds. However, it is poorly understood to what extent the departure decisions are more influenced by some parameters in relation to others, and how they interact with each other. We explored here how fuel load, date, rain and wind (measured on the ground and at high altitude, codified as a tailwind component) influenced the departure decisions of migratory Blackcaps (*Sylvia atricapilla*) from a stopover site. We used mark–recapture data of 947 Blackcaps collected during the autumn migration period 2005 at a stopover site in northern Iberia, estimating the emigration likelihood with Cormack-Jolly-Seber models, in which we tested for the effect of these four study variables. Best models fitting data showed an additive and positive effect of tailwind and fuel load on the emigration likelihood.

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Zusammenfassung Die meteorologischen Verhältnisse, der Energievorrat sowie das konkrete Datum können bei Zugvögeln die Entscheidung darüber beeinflussen, wann sie ihren Zug beginnen, bzw. fortsetzen. Dabei ist jedoch nur wenig dazu bekannt, in welchem Ausmaß welcher dieser Parameter relativ zu den anderen die Abflugentscheidung beeinflusst und inwieweit sie untereinander interagieren. In dieser Studie haben wir für ziehende Mönchsgrasmücken (*Sylvia atricapilla*) untersucht, wie ihr Energievorrat, das jeweilige Datum, Regen und Wind (gemessen am Boden und in größerer Höhe, angegeben als Rückenwindkomponente) die Entscheidung für den Weiterflug von einem Zwischenstop beeinflussten. Hierfür verwendeten wir die Daten von 947 markierten Mönchsgrasmücken, die während des Herbstzuges 2005 in einem Zwischenstop-Gebiet im Norden der iberischen Halbinsel wiedergefangen wurden. Die Weiterzug-Wahrscheinlichkeit wurde anhand von Cormack-Jolly-Seber-Modellen abgeschätzt, mit denen wir die möglichen Auswirkungen der vier untersuchten Variablen testeten. Das den Daten am besten angepasste Modell zeigte einen additiven, positiven Effekt von Rückenwind und Energievorrat auf die Weiterzugswahrscheinlichkeit.

Introduction

Meteorological conditions have well documented to influence avian migration, both during flight and when birds must decide to depart from, or remain at, a stopover site

(Lack 1960; Alerstam 1990; Richardson 1990; Elkins 1999; Liechti 2006). Parameters such as wind, rain and clouds are determinants for departure decisions. Thus, passerines tend to depart and fly with no rain, no or few clouds and with tail wind assistance (Åkesson and Hedenström 2000; Åkesson et al. 2001, 2002; Barriocanal et al. 2002; Erni et al. 2002; Schaub et al. 2004).

Data used to date to analyse the effects of weather on departure decisions come from three main sources: (1) direct observations (counting) of departing specimens (Hebrard 1971; Chan 1995; Bolshakov and Rezvyi 1998; Bolshakov and Bulyuk 1999), (2) timing of departure of individually marked specimens, either ringed (Fransson 1998; Dänhardt and Lindström 2001; Bulyuk and Tsvey 2006) or equipped with a radioemitter (Åkesson and Hedenström 2000; Åkesson et al. 2001, 2002; Bolshakov et al. 2007; Tsvey et al. 2007), and (3) estimations of the emigration likelihood (equivalent to the departure one) using Cormack-Jolly-Seber (CJS) models (Schaub et al. 2004), which are based on mark–recapture data. A constraint with the use of direct observations is that number of departing specimens is related to that of stopping-over ones. Unfortunately, this last may be unknown, so the use of direct counts on departing birds could entail some biases. The use of the last re-sighting of a marked bird to assess departure date could also entail biases, since birds could remain at a stopover site for some time after their last capture (or re-sighting) (Schaub et al. 2001; but see Bayly 2007). Following birds with radio transmitters is a good solution, though sample sizes are often small, and obtaining data is very time-consuming. By contrast, the use of CJS models allows estimating survival (i.e., permanence at a stopover site; Φ), and hence the emigration likelihood (ε, defined as $1 - \Phi$) with relatively less sampling effort, smaller budget, and larger sample size (Schaub et al. 2004). Moreover, these models allow the estimating of the emigration likelihood independently from the recapture one (p). However, CJS models can overestimate the emigration likelihood (Schaub et al. 2004), e.g., if there is a marked change in weather from one day to the next, as models cannot estimate the exact day of departure, just the emigration likelihood within a window of days.

In general, rain has been reported to have a strong effect on departure decisions, migrant birds tending to depart in nights with no rain (reviewed by Lack 1960; Alerstam 1990). Wind assistance at ground can affect departure decisions (Åkesson et al. 2001, 2002), although some other studies found that the only relevant winds are those at some altitude above ground level, from 300 m (Schaub et al. 2004) up to 3,000 m (Barriocanal et al. 2002; see also, for a review, Liechti 2006). Since wind flow at ground level can change in relation to topography, with the possibility of different wind directions at different altitudes (Schaub et al. 2004), local differences could be enough to explain these results. Also, it is possible that birds could take into account different weather variables depending on whether they are on the autumn or spring migrations (Cochran and Wikelski 2005).

Contrasting with wind or rain, which could be considered as environmental or exogenous variables, those associated with the circannual time programme may be considered as endogenous ones (Bulyuk and Tsvey 2006). A possibility for analysing the influence of the endogenous circannual time programme would be to test for the effect of timing (date) on departure decisions. Thus, birds arriving later in the season may give a different response to environmental cues than those passing over earlier, which would have more time to reach their goal areas. Furthermore, birds migrating later would be under much stronger time constraints, and their decisions could be more independent of exogenous variables en route (Jenni and Schaub 2003). This should be particularly marked in migrants minimising the duration of their migration (Alerstam and Linström 1990).

A bird may also use its own fuel load as a factor in deciding whether to depart from a stopover site or to remain at it. Theoretically, a bird arriving at a stopover site with a high fuel load would be ready to continue its migration and, therefore, should be expected to stopover for shorter periods, hence being more motivated for departing (Alerstam and Linström 1990; Moore and Aborn 1996). In line with this reasoning, Arizaga et al. (2008) observed that stopover duration was negatively correlated with fuel load (measured at first capture event) in migrating Blackcaps (*Sylvia atricapilla*). However, other authors found no clear correlations between arrival fuel load and stopover duration (Bulyuk and Tsvey 2006; Tsvey et al. 2007). To what extent these differences could be due to a highly adaptable individual behaviour or to a hierarchical consideration of those variables governing the departure decisions is still a question that is scarcely understood.

Both the exo- and endogenous parameters can affect the departure decisions, though their importance could be different. In this sense, three hypotheses may be put forward. First, birds could pay more attention to exogenous variables such as rain, wind or fuel load. Although fuel load is determined internally (Berthold 1996), it is affected by many external elements, such as food availability, food access, predators, etc. (Newton 2008), and we should thus consider this variable as an exogenous factor in comparison with endogenous factors such as date. In this scenario, it should be expected that even migrants with larger fuel loads may delay their departure until they have favourable weather. Second, departure decisions could depend only on endogenous parameters. In this case, migrants will depart even if they have to face non-favourable weather conditions, and to use more energy for flight (i.e. to increase their flight costs). This predominance of endogenous control in the departure decisions has been observed during the spring migration period, when the urge to reach goal areas is stronger than during autumn (Gauthreaux 1971; Hebrard 1971; Cochran 1987). Third, the emigration likelihood may be influenced by both exo- and endogenous parameters. In this case, their effect could be either additive (e.g. given a value of a factor, the emigration likelihood may decrease, or increase, for a given value of a second factor), or the variables may interact with each other (i.e. the response for a given factor could be different for different values of a second factor). In this case, both exo- and endogenous parameters controlling for migration may be more or less balanced.

The Blackcap is an abundant Palaearctic songbird, breeding from western Europe to western Asia (and also in Macaronesia), mainly within the Euro-Siberian region (Cramp 1992). In western Europe it behaves as a partial migrant, with many populations or individuals from northern and central Europe overwintering within the circum-Mediterranean region (Shirihai et al. 2001). Like many insectivorous passerines, it is a nocturnal migratory bird, and abandons stopover places during the twilight period after sunset (Moore 1987).

The aim of the study was to analyse the relative effects of exo- and endogenous factors on departure decisions of migratory Blackcaps at a stopover site in northern Spain during the autumn migration period.

Methods

Sampling area

Blackcaps were mist-netted at a Constant Effort Site (CES) at Loza (42°50′N, 01°43′W), 40 km south of the western Pyrenees, in northern Iberia. This CES is placed in a ca. 40-ha area formed by prairies and shrubs, used by a number of passerines as a stopover area (Arizaga et al. 2008). The population breeding at Loza is quite small and, during the migration period, most captures are migrants from abroad (>98%; J.A., unpublished data). No wintering Blackcaps have been detected at Loza (J.A., unpublished data).

Data used here [947 different Blackcaps, 61 (6.4%) recaptures] were obtained during the autumn migration period, from 12 September to 27 October 2005, when we performed daily trapping sessions. Each Blackcap was individually ringed and its sex and age determined following Svensson (1998). We measured wing length (±0.5 mm; method III from Svensson 1998), body mass (±0.1 g accuracy; TANITA digital balance) and fat scores (scaled from 0 to 8, following Kaiser 1993).

Meteorological data

Meteorological data used here obtained from (1) Arazuri Meteorological Station (rain and wind at 2 m above ground level), placed 3.5 km south of Loza (42°48′N, 01°43′W), and (2) NOAA, National Oceanic and Atmospheric Administration, U.S. Department of Commerce (wind at a pressure of 925 mb, equivalent to an altitude of ca. 300–400 m above ground level). As a nocturnal migratory bird, a Blackcap will consider meteorological conditions around sunset, so, regarding rain, it was calculated for each day from 1800 to 2200 hours, corresponding to 2 h before sunset to 2 h after, and for wind above ground level, at 1800 hours (NOAA only provides precise data for each 6-h interval from 0000 hours onwards). Data on rain (originally in mm) were codified as a binomial variable (i.e., rain >0 mm or no rain during these 4 h). Wind features (direction measured over 360°, as the direction the wind comes from, so 0 and 360° refer to winds with a northerly component; velocity in m/s) were integrated as a tailwind component (b), following:

$$b = V \cos[\alpha_T - (180^\circ + \alpha_W)] \quad (1)$$

where V was the wind velocity, α_T the (presumed) departure direction (200°, according to data on recoveries of migratory Blackcaps ringed during the autumn migration period at Loza; J.A., unpublished data), and α_W the direction the wind comes from (Åkesson and Hedenström 2000). High, positive tailwind components correspond to situations of a strong tailwind, whilst high, negative values correspond to strong headwind.

Data analyses

CJS models were used to analyse capture–recapture data. Overall, our matrix had a size of 947 rows (individuals) and 46 columns (sampling days).

Before starting to select CJS models, we explored the fit of the data to CJS assumptions. With this goal, we used a goodness-of-fit (GOF) test. The GOF test on a CJS model where both ε and p (emigration and recapture likelihoods, respectively) were time-dependent [$\varepsilon(t)\ p(t)$] was carried out with U-CARE software (Choquet et al. 2001), allowing us to also identify a basic starting model that fits the data from which to start model selection. The overall GOF test for the emigration dataset was not significant ($\chi^2_{80} = 36.308$, $P = 0.999$). The occurrence of transients (i.e., birds that leave a stopover locality almost immediately after arriving; e.g. Schaub et al. 2004) breaks CJS assumptions (Pradel et al. 1997; Belda et al. 2007). For transients, their survival after the first marking event would be zero, and this would bias the emigration likelihood, since these birds could leave the stopover locality independently of weather. Test 3SR, one of the components of GOF, is used to test for the lack of homogeneity in survival among birds, depending on whether or not they had been caught previously. Hence, this test is significant in case of occurrence of transients. In addition, U-CARE provides a specific test for transience. Overall, Test 3SR was non-significant ($\chi^2_{28} = 9.144$, $P = 0.999$), as did not the positive z statistic for transience either ($\chi^2_{28} = 1.131$, $P = 0.258$). Thus, the most complex model with which to start to model emigration likelihood was the one in which both ε and p were time-dependent [$\varepsilon(t)\ p(t)$]. All other fitted models were nested within our starting one.

To test for the effects of each variable on the emigration likelihood, fuel load and date were included as covariates in the dataset. We expressed fuel load as body mass (measured at first capture event) divided by tarsus length, this last used as an estimate of body size (Senar and Pascual 1997). Indeed, when regressing body mass on tarsus length in birds without any visible fat content (data from autumn 2003–2006 at Loza; moulting birds excluded; $n = 32$), we obtained a higher correlation ($r = 0.618$, $P < 0.001$) than when regressing body mass on wing length ($r = 0.473$, $P < 0.001$). Moreover, rain and tailwind were included in the time-dependent models. Stopover duration is also a relevant variable determining departure decisions, since birds which would have stopped over for longer may be more motivated to depart (Bulyuk and Tsvey 2006; Bolshakov et al. 2007; Tsvey et al. 2007). However, our dataset was too small to also consider this variable. If weather is relevant, the emigration likelihood should increase in nights with no rain and a tailwind. In relation to fuel load and date, we should expect an increasing emigration likelihood among those birds with more fuel or arriving late within the season (i.e., more time-stressed).

We modelled the emigration likelihood by incorporating the individual covariates and the interactions between them into the modelling (White and Burnham 1999). The logit-link function establishing the relationship survival–covariates was used in the models:

$$\mathrm{Logit}(\Phi) = B_0 + B_1(\text{covariate}) \qquad (2)$$

ε is $1 - \Phi$, hence,

$$\varepsilon = 1 - \frac{e^{B_0 + B_1(\text{covariate})}}{1 + e^{B_0 + B_1(\text{covariate})}} \qquad (3)$$

where the logit-scale coefficients (hereafter, B parameters) are constant. To ensure that numerical optimisation algorithm found the correct B parameter estimates, individual covariates were standardised using the option “Standardise Individual Covariates” from MARK (Schwartz et al. 2005). When selecting the best model that fits the data, we only considered those models where B parameters differed (significantly) from zero (Franklin 2001). Thus, we considered that when the 95% confidence interval of a B parameter included zero, it showed no significant effect on that covariate (e.g. Taylor et al. 2004; Greño et al. 2008).

The Akaike’s Information Criterion (AIC) was used for ranking the fit of the models to the data (Burnham and Anderson 1998). The lowest AIC value was found in that model best fitting the data. We considered that models with a difference in AIC below two units (ΔAIC <2) were similar to each other, whilst a ΔAIC >2 indicated real and significant differences in the fit of the models to the data (Burnham and Anderson 1998). The weight of the models was the likelihood that they fitted the data better. Moreover, we summed AIC weight across all models that included a variable (e.g. wind) to estimate the relative likelihood of that variable being included in the best models. Altogether, we considered 32 models (Table 1). Models with triple or

Table 1 Models (ε refers to emigration likelihood, and p to likelihood of capture) of the emigration likelihood of migratory Blackcaps (*Sylvia atricapilla*), at a stopover locality in northern Iberia, in relation to fuel load, date, rain and tailwind, at both low (2 m) and high (300 m) altitude

Models	AICc	ΔAICc	AICc weight	No. of parameters	Deviance
1. $\varepsilon_{\text{fuel+wind(2)}}, p$	732.26	0.00	0.173	4	724.22
2. $\varepsilon_{\text{fuel+rain+wind(2)}}, p$	733.39	1.14	0.098	5	723.33
3. $\varepsilon_{\text{fuel+date+wind(2)}}, p$	733.51	1.26	0.092	5	723.45
4. $\varepsilon_{\text{fuel*wind(2)}}, p$	733.60	1.34	0.088	5	723.54
5. $\varepsilon_{\text{fuel+wind(300)}}, p$	733.79	1.53	0.080	4	725.75
6. $\varepsilon_{\text{wind(2)}}, p$	735.19	2.94	0.040	3	729.17
7. $\varepsilon_{\text{rain*wind(2)}}, p$	735.29	3.04	0.038	5	725.23
8. $\varepsilon_{\text{fuel*wind(300)}}, p$	735.47	3.21	0.035	5	725.41
9. $\varepsilon_{\text{fuel+date}}, p$	735.56	3.30	0.0331	4	727.52
10. $\varepsilon_{\text{fuel}}, p$	735.64	3.38	0.03185	3	729.61

Of 32 fitted models, only the best ten are shown. We show the Akaike’s Information Criterio (*AICc*), the difference of AICc of each model with respect to the first one and the AICc weights higher interactions were not considered due to a sample size constraint.

Mean values are given ±SE.

Results

Weather and fuel load of Blackcaps at Loza

During the 45 days used to estimate the emigration likelihood (that of 27 October was not considered), and for the specific time before/around sunset, mean tailwind at 2 m above ground level was 0.62 ± 0.24 m/s (range: -2.94 to 4.14 m/s), and at ca. 300 m above ground level, -0.93 ± 0.67 m/s (range: -11.7 to 11.6 m/s). Moreover, distribution of wind directions was not homogeneous, with dominant tailwind during early autumn, and dominant headwind during late autumn (Fig. 1). Tailwind values at 2 and 300 m above ground level were positively correlated ($r = 0.614$, $p < 0.001$). Between 1800 and 2200 hours, it rained on 6 (13.3%) out of 45 days.

Mean relative body mass of the Blackcaps was 0.922 ± 0.003 g/mm (range: 0.241–1.342; $n = 947$).

Effects of fuel load, date, rain and wind on departure decisions

Overall, recapture likelihood (p) was best estimated when the constant model was taken into account [$\varepsilon(t)\,p(.)$ vs. $\varepsilon(t)\,p(t)$], being $p = 0.021 \pm 0.004$ for the model $\varepsilon(t)\,p(.)$. The model which best fitted the data was the one in which the emigration likelihood was an additive function of fuel and wind at ground level (Table 1), thus indicating that these two exogenous variables had a major effect on departure decisions of Blackcaps. Nonetheless, models 2–5 showed a difference in AICc <2 from model 1 (Table 1), so they did not differ significantly from that model. Fuel was the only factor shared by models 1–5, and tailwind at ground level was included in models 1–4. Tailwind at high altitude was only included in model 5.

Looking at Beta parameters of model 1, we observed that both fuel load and tailwind at ground level were positively correlated with the emigration likelihood (i.e. the higher the fuel load and the tailwind factor, the higher the emigration likelihood) (Table 2). Moreover, rain and date were also positively correlated with the emigration likelihood (i.e. emigration likelihood was a bit higher in the case of rain and during late autumn than in the case of no rain and during early autumn). However, a more detailed analysis of Beta parameters showed that, in models 2 and 3, both rain and date were non-significant (Table 2), suggesting a null or weak effect on the emigration likelihood. Indeed, the sum of AIC weights in models that included fuel was 0.740 compared with 0.605 in models that included wind at ground level. Conversely, this value was lower in models that included rain (0.270), date (0.263) and wind at high altitude (0.237).

Models 1–4 were averaged to explore how factors were related among them (Fig. 2). Thus, the emigration likelihood was observed to increase with increasing fuel load, with the slope more marked in case of tailwind. Moreover, the emigration likelihood was higher with tailwind (+1.5 m/s in Fig. 2) than with headwind (−1.5 m/s in Fig. 2), independently of fuel load. Effect of wind at high altitude on departure decisions was similar to the one observed for wind at ground level (Fig. 3).

Discussion

Cormack-Jolly-Seber (CJS) models were used to analyse the relative importance of exo- and endogenous parameters in the emigration likelihood of migratory Blackcaps at a stopover site during the autumn migration period. Our results support the hypothesis that departure decisions were affected by two exogenous variables, fuel load and wind at ground level and, to a lesser extent, wind at high altitude. Previous analyses had not considered jointly the effects of these parameters on departure decisions (Åkesson et al. 1996, 2001, 2002; Åkesson and Hedenström 2000; Dänhardt and Lindström 2001; Schaub et al. 2004; Tsvey et al. 2007). The models that best fitted the data (once averaged) showed an additive effect of each variable.

The emigration likelihood was positively correlated with fuel load, measured at the first capture event. Thus, birds caught with higher loads of fuel showed a higher likelihood of abandoning the stopover locality. As Blackcaps have been observed to gain fuel at a constant rate at Loza (Arizaga et al. 2008), this agrees with the fact that the stopover duration may be negatively correlated with fuel load when arriving. For a bird arriving at a stopover site carrying enough fuel to continue to its next goal area without needing to refuel, it could be more advantageous to depart and follow its migration than remain at that stopover site. In addition, birds with more fuel would be more able to successfully overcome bad weather conditions, as they would have a safety energy margin to continue flying without needing to land at a stopover site to refuel. In other small European birds, such as Robins (*Erithacus rubecula*), the stopover duration was uncorrelated with fuel load at arrival (Tsvey et al. 2007). Reasons suggested to explain these results were strong endogenous spatio-temporal programmes, high predictability of good stopover localities at the next target localities, or a handling effect (Tsvey et al. 2007).

For given fuel loads, the higher the tailwind (both at ground level and high altitude), the higher the emigration likelihood. Thus, for a fuel load of 1.00 g/mm, the

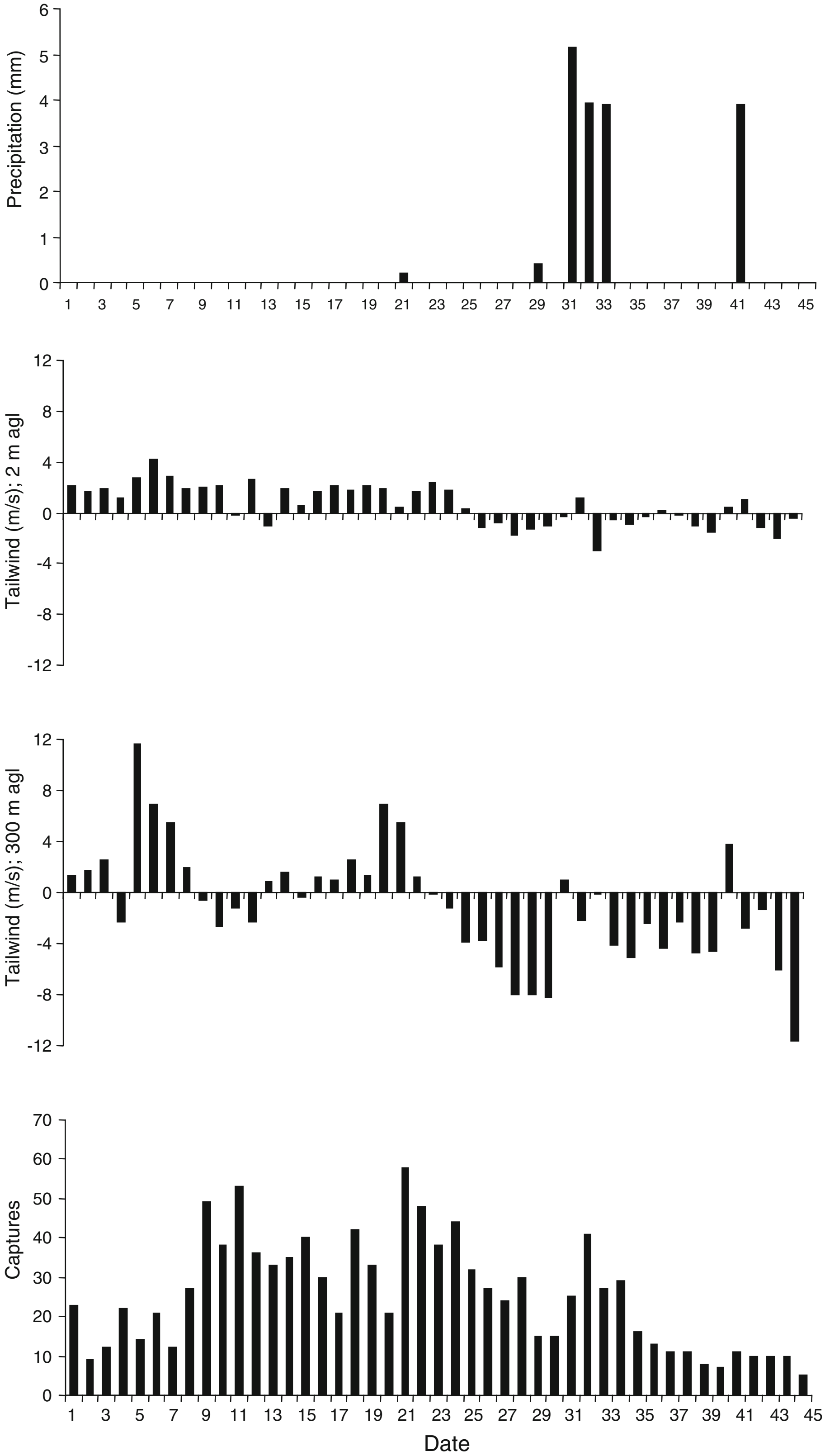

Fig. 1 Number of captures of Blackcaps (*Sylvia atricapilla*), rain and wind conditions (measured at 2 and 300 m above ground level) at Loza during autumn 2005, at 1800 hours (ca. 2 h before sunset)

emigration likelihood was nearly 0.10 (in the case of headwind at ground level: −1.5 m/s) or 0.20 (in the case of headwind at high altitude: −6.0 m/s), and 0.40 for tailwind at both ground level and high altitude (+1.5 and +6.0 m/s), supporting the suggestion that departure decisions of migrating Blackcaps were to some extent influenced by

Table 2 Standardised Beta parameters for those models where the difference in AICc with first (best) model was below 2

Models	Parameters	Beta	SE	95% confidence interval	
				Lower	Upper
1. $\varepsilon_{\text{fuel+wind(2)}}$, p	Fuel	0.262	0.121	0.025	0.500
	Tailwind (2 m)	0.262	0.114	0.038	0.486
2. $\varepsilon_{\text{fuel+rain+wind(2)}}$, p	Fuel	0.264	0.123	0.022	0.506
	Rain	0.713	0.700	−0.658	2.085
	Tailwind (2 m)	0.352	0.162	0.036	0.669
3. $\varepsilon_{\text{fuel+date+wind(2)}}$, p	Fuel	0.246	0.120	0.010	0.482
	Date	0.208	0.234	−0.250	0.667
	Tailwind (2 m)	0.404	0.199	0.013	0.795
4. $\varepsilon_{\text{fuel*wind(2)}}$, p	Fuel	0.214	0.131	−0.042	0.471
	Tailwind (2 m)	0.269	0.115	0.043	0.494
	Fuel × Tailwind (2 m)	0.122	0.147	−0.166	0.409
5. $\varepsilon_{\text{fuel+wind(300)}}$, p	Fuel	0.233	0.118	0.001	0.465
	Tailwind (300 m)	0.080	0.041	0.000	0.159

Models numbered as in Table 1

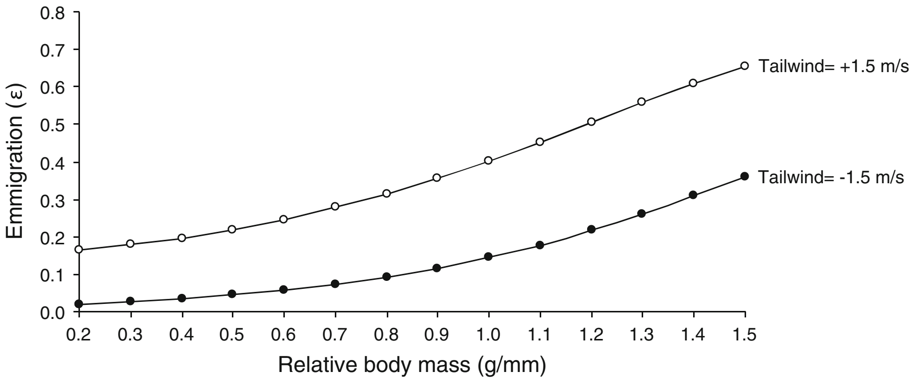

Fig. 2 Relationship between the emigration likelihood, fuel load and tailwind at 2 m above ground level,averaged from models 1–4 (numbered as in Table 1). Because date and rain had an irrelevant effect on the emigration likelihood (Table 2), they have not been considered in this figure

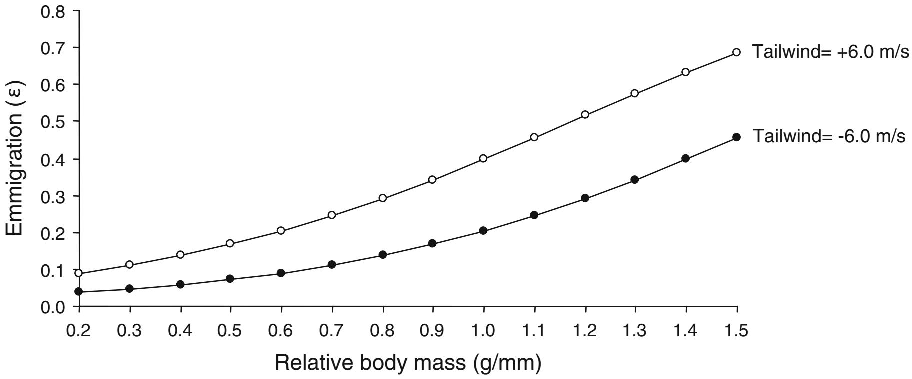

Fig. 3 Relationship between the emigration likelihood and fuel load, for different tailwinds at 300 m above ground level, as deduced from model 5 (numbered as in Table 1)

tailwind whatever the altitude. Erni et al. (2002) demonstrated that only headwinds ≤5 m/s are unfavourable and, therefore, that better conditions are good for migration. Thus, the headwind measured at ground level was never below −5 m/s, suggesting that, at this altitude, birds never had unfavourable wind conditions during our autumn migration period. However, our birds did react to tailwinds of different directions, and hence the emigration likelihood was close to zero in the case of a headwind and low fuel load, whilst it was nearly 0.20 in the case of a tailwind and low fuel load. It cannot be completely rejected that these results could be masked by a tailwind at high altitude, which was often ≤5 or >5 m/s. In other words, our birds may be affected by wind at high altitude rather than wind at ground level but, since both winds were correlated, it is impossible to separate both effects in models.

Wind conditions on the ground have been reported to have both a low (Schaub et al. 2004) and high effect

(Åkesson and Hedenström 2000; Åkesson et al. 2002) on departure decisions. In these last cases, however, the authors did not test for interactions between wind and the rest of parameters considered here, so this comparison should be considered with caution. It is likely that local topography could be a key factor for the wind at ground level being a relevant variable in relation to departure decisions of migrants from a stopover site. In line with this, Schaub et al. (2004) found that birds did not consider wind features at ground level, but at 300 m above it. Because of the topography of each site, wind conditions are not always the same at different altitudes (Schaub et al. 2004). Thus, when wind conditions at ground level differ from wind conditions at high altitude, it could be stated that migrants tend to be influenced by those at high altitude, which was not the case at Loza.

To what extent a bird on land is able to distinguish wind conditions at different altitudes and, particularly, which are the clues that birds consider to make proper departure decisions, and which are the senses implicated in perceiving these clues, is a question still poorly known (but see Åkesson et al. 2002).

Timing within the season had a very weak effect on the emigration likelihood, as did rain. Clearly, this disagrees with other studies based on CJS models (Schaub et al. 2004), as well as on direct observations (Bolshakov and Rezvyi 1998; Bolshakov and Bulyuk 1999) or radar-based studies (Erni et al. 2002), where rain has been reported to keep migrants at stopover localities. It is possible that our results may be biased by the fact that the number of days with rain was very low (only 6 out of 46) and were concentrated at the end of the season.

Overall, our results suggest that migrants consider more than a single key factor when they must decide to depart from a stopover site, or remain at it (Dierschke and Delingat 2001). In particular, the response was affected by actual values of fuel load and, secondly, wind (tailwind). The departure decisions, in conclusion, were influenced by mainly exogenous variables. Endogenous parameters (here date, used as a surrogate for internal rhythms) did not have any biologically significant effect on departure decisions of Blackcaps. Thus, although the progress of migration is to some extent endogenously determined (Berthold 1996), exogenous variables such as wind and fuel load had a much stronger effect on departure decisions of Blackcaps. Whether such behaviour is generalised for migrants passing through northern Iberia or southern Europe is something that requires further research, and it may be associated not only with the specific ecological requirements of each species when stopping-over but also with the distance to the species and/or population-specific target wintering area and the corresponding time-constraints that could exist in relation to this distance. A higher time-constraint could give more importance to the endogenous parameters determining departure decisions. How other parameters could interact with those analysed here and determine the departure decisions (e.g. food availability, time already spent at given stopover sites or predators) is a question that also still needs further studies.

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