When to depart from a stopover site? Time-since-arrival matters more than weather conditions

Sébastien Roques [1,2], Pierre-Yves Henry[3,4], Gaétan Guyot[5], Bruno Bargain[5], Emmanuelle Cam[2,6], Roger Pradel[1]

[1]CEFE, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier - EPHE, Montpellier Cedex 5 France

[2] Laboratoire Evolution et Diversité Biologique, UMR CNRS 5171, Bât 4R1, 118 route de Narbonne, Université Toulouse 3, Paul Sabatier, 31062 Toulouse Cedex 09, France

[3] Mécanismes adaptatifs et Evolution (MECADEV UMR 7179), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, 1 avenue du Petit Château, F-91800 Brunoy, France

[4] Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO), Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Bâtiment 135, CP135, 43 rue Buffon, F-75005 Paris, France

[5] Bretagne Vivante, 19 rue de Gouesnou - BP 62132, 29221 BREST CEDEX 2, France

[6] Univ Brest, CNRS, IRD, Ifremer, LEMAR, F-29280 Plouzané, France

Correspondence author: Sébastien Roques

E-mail: sebastien.roques@cefe.cnrs.fr

ORCID ID : 0000-0003-3618-0747

Abstract

On their journey to wintering or breeding sites, migratory birds usually alternate between migratory flights and stopovers where they rest and refuel. Actually, migrating birds spend most of the time at stopovers. Consequently, selection to minimize total time spent on migration likely operates mainly on the effectiveness of stopover rest and refueling. Departure probability from stopover sites depends both on weather conditions and fuel stores, but their respective role has not been quantified. In the present study, we assess the relative contribution of factors driving the departure decision from a stopover site. As we cannot reliably characterize body condition and restness when capture probability is low, we propose to use the Time Since Arrival (TSA) as a proxy of the changes through days of the internal state of stopovering birds. We developed a specific capture-recapture model to quantify the relative contribution of TSA and climatic conditions on a 20-year capture-recapture dataset of a long-distance migratory songbird (Sedge warbler). The effect of TSA has yet the major contribution to departure probability compared to weather conditions. Here, low humidity and an increase of atmospheric pressure in the days preceding departure are the weather conditions associated with a higher departure probability but remain secondary compared to the time the individual has already spent at the site. The probability to depart from a stopover site is therefore largely determined by the time that a bird has already spent at the site. Whether this Time Since Arrival is rather a proxy of resting, feeding or fattening efficiency remains to be explored.

Keywords: Stopover, Time Since Arrival, Capture-Recapture, Sedge warbler, Bayesian inference

1. Introduction

Each year migratory birds species commute between breeding and wintering areas (Hahn et al. 2009). Most of the species cannot go from breeding to wintering grounds in a single flight of

thousands of kilometers. They must stop to rest, feed and refill energy stores regularly (Alerstam 1990, Åkesson and Hedenström 2007). The duration of migratory flights and stopovers determines the total duration of the journey. The optimal migration theory proposes that the total time spent on migration is the performance under selection (Alerstam, 1990; Alerstam, 2011). To maximize survival, individuals must optimize their journey to match with seasonal variation in food availability (and their energy requirements) at stopover sites and to arrive at wintering or breeding areas when resource availability is sufficient (Alerstam 1990, Sanz et al. 2003, Prop et al. 2003, Baker et al. 2004, Becker et al. 2008). Birds spend much more time at stopover sites than in migratory flight, with almost 85% of the journey spent on stopover (Hedenström and Alerstam 1997, Green et al. 2002, Schmaljohann et al. 2012). Consequently, selection to minimize total time spent on migration likely operates mainly on the effectiveness of stopover rest and refueling (Hedenström and Alerstam 1997).

Deciding to leave the stopover site normally means a new flight of hundreds of kilometers. This movement itself, and its termination, are highly constrained by the maximal flight capacity (given the size of energy reserves) and atmospheric conditions (Alerstam, 1990; Jenni & Schaub, 2003; Schmaljohann & Eikenaar, 2017; Wikelski et al., 2003). Once settled at a stopover site, the duration of the stay depends on factors associated with the initiation of movement (i.e. to depart from the site). This probability to depart depends on fuel store, resting state, food availability, weather conditions and migratory experience (Jenni and Schaub 2003, Schmaljohann and Eikenaar 2017).

Recent studies have tried to disentangle the environmental factors driving the departure decision (Schaub et al. 2008, Ktitorov et al. 2010, Arizaga et al. 2011, Deppe et al. 2015, Dossman et al. 2016, Schmaljohann and Eikenaar 2017). Departure decision depends on wind speed and direction (tailwind assistance reducing the cost of flight; Tsvey et al. 2007, Arizaga et al. 2011, Ma et al. 2011, Dossman et al. 2016) and rainfall or humidity which usually force

birds to stay at the stopover site (Tsvey et al. 2007, Arizaga et al. 2011, Deppe et al. 2015, Dossman et al. 2016). Cloud cover also influences departure decision decreasing the visibility and hence the ability of birds to navigate (Zehnder et al. 2001, Åkesson and Hedenström 2007).

The internal state (resting state, fuel store, migratory experience) of the individual also influences the departure decision: birds need to rest and reach a sufficient level of fuel store to perform the next migratory flight (Alerstam 1990, Hedenström and Alerstam 1997, Schaub et al. 2008, Goymann et al. 2010, Schmaljohann et al. 2012, Dossman et al. 2016, Schmaljohann and Eikenaar 2017). Apart from resting to recover from extreme physical exercise and sleeping to recover from sleep deprivation during migratory flight (Schwilch et al. 2002), birds at stopover allocate most of their time and energy to foraging (Hedenström and Alerstam 1997). They are assumed to re-fill their energy stores as fast as possible, and to continue their migratory journey whenever the weather conditions are favorable. Also, songbirds experiencing migration for the first time (juveniles) and those who have already performed former travel to wintering areas (adults) may behave differently regarding departure decisions (Deppe et al. 2015, Dossman et al. 2016).

To our knowledge, the relative importance of bird internal state (resting state, fuel store) *versus* weather conditions at determining departure has never been assessed using a same modeling framework. Also, the contrasted results obtained concerning the relationship between fuel store and departure probability in previous studies could be due to different local constraints or the poor robustness of measures of fuel store at the only occasions when the individual is captured. The lack of an appropriate method to jointly incorporate these factors in a same capture-recapture (CR) framework could also explain these results (Jenni and Schaub 2003, Schmaljohann and Eikenaar 2017). To get around these concerns we defined a variable: the time that the individual has spent at the stopover site since its arrival (Pledger et al. 2008). Since birds need to rest after a long distant migratory flight and that fattening increases with the

duration of the stay at stopover (Alerstam 1990, Schwilch and Jenni 2001, Jenni and Schaub 2003, Schaub et al. 2008, Schmaljohann and Eikenaar 2017), we hypothesize that developing a reliable estimate of the Time Since Arrival (TSA) is a means of having a good proxy of the overall progress of the internal state of the stopovering bird, and could be used as a proxy to investigate the influence of internal state on departure probability. The time the individual has spent at the site must be estimated using an analytical technique accounting for the daily capture probability of marked individuals (i.e., the probability of capturing an individual that is alive and present in the site). This was a methodological challenge because investigators cannot know exactly neither the day when a bird arrives nor the day when it departs from the site. Many stopover studies have relied on the assumption that birds are captured for the first and last time on the exact days of arrival and departure from the site. This assumption is unrealistic: the probability that a bird is captured in a given day usually lies between 0.1 and 0.2, and the resulting "minimal stopover duration" (duration between first and last captures) strongly underestimates the actual stopover duration (by a factor that may be as large as 3; Schaub, Pradel, Jenni, & Lebreton, 2001). Thus, we developed a method that allows to model departure probability as a function of the estimated TSA and environmental covariates.

In the present study, we addressed the relative contribution of the Time Since Arrival and meteorological conditions to the departure decision. Specifically, we developed a capture-recapture model allowing the estimation of TSA and the effect of weather conditions in order to analyse a long-term CR dataset on a long-distance migrant passerine at a stopover site. We hypothesized that TSA will be the main driver of the departure decision for a long-distant migrant and that wind, humidity, cloud cover and atmospheric pressure will have a lower, but significant effect on the departure decision. Also, hypothesizing that stopover duration may differ according to migratory experience, we tested for differences in stopover duration between juveniles and adults (Deppe et al. 2015).

2. Material and methods

2.1 Study area, sampling and dataset

The study site is the Trunvel ringing station (Tréogat, Brittany, France; 47.8964859, -4.3698274). Data from marked individuals have been collected using a standardized mist-netting protocol (including tape-luring; B. Bargain, C. Vansteenwegen, & J. Henry, 2002). Each captured bird was identified, ringed and aged. The study period is from the 1st to the 30th of August every year. The Sedge warbler (*Acrocephalus schoenobaenus*) is the most abundant species that stops-over at this site during its journey to winter quarters in sub-Saharan Africa. This 12-g songbird strictly depends on reedbeds where it essentially forages on one aphid species (*Hyalopterus prunii*) to re-fill energy stores (Bibby and Green 1981).

Between 1986 and 2014, 79,700 individuals have been marked (Dehorter and CRBPO 2015). Among all migrant songbirds that land at a site, only a small fraction stays several days to rest and refuel (i.e. actual stopover; Warnock, 2010). The majority either continues migration by the following night, or moves to another stopover place (i.e., transients; Bächler & Schaub, 2007; Schaub et al., 2008). As we aim to study the departure probability of birds that stayed over at the site, we analyzed only capture-recapture data of birds that were caught at least twice during a season (including recaptures during the same day). Hence, the estimated stopover duration applies only to the part of the population passing by the site and that stays for at least some hours or days. The final sample for analyses included data from 683 adults and 4927 juveniles, that had their latest recapture at the site on average 3.4 ± 3.6 (SD) days after their first capture. The mean mass gain between first and last capture on individuals was 0.48g ± 1.48 (SD).

2.2 Weather conditions

Weather variables expected to influence daily departure probability (between day t-1 and t) were: (i) wind (on day t-1), (iii) relative humidity (on day t-1), (iii) cloud cover during the night [i.e. between day t-1 and t; scale from 0 (no cloud) to 8 (complete sky cover)] (iv) atmospheric pressure; as birds likely perceive changes in pressure rather than pressure itself, we used the change in atmospheric pressure between the current day t and day t-1 as covariate (denoted as $\Delta Pressure$ in hPa). Depending on its direction, wind can either facilitate flight (tailwind) or increase the cost of flight (headwind). To integrate both wind effects, the wind covariate was computed as (Arizaga et al. 2011):

$$wind = Vcos[\alpha_T - (180° + \alpha_W)],$$

where V is wind speed (in $m.s^{-1}$), α_T the assumed departure direction (120° according to recovery data; note that birds would not cross the Bay of Biscay, Dehorter and CRBPO 2015, so 120° is almost the coast direction), and α_W the direction the wind comes from (Åkesson et al. 2002). Since birds depart on migration at the end of the day (Bibby and Green 1981), we used wind speed and direction between 2 hours before sunset on day t-1 until the middle of the night on day t. All weather covariates were scaled prior to the analyses. The weather data comes from the Penmarch meteorological station (47.797537, -4.374768).

2.3 Modeling & statistical analyses

We used a formulation of the Jolly-Seber (JS) model (Jolly 1965, Seber 1965) parameterized with entry probability in the sampling area (Crosbie and Manly 1985, Schwarz and Arnason 1996). This allows modeling the arrival of birds at the stopover site. This formulation has already been used to estimate population size and stopover duration of birds at a site (Lyons et al. 2016). As we had no count of unmarked birds in our study, we adapted this model to the use of marked birds with at least one local recapture. The parameters of the model are:

ϕ_t Probability of staying in the sampling area between day *t* and *t+1*

η_t Probability of arriving at the stopover area at day *t* given that the individual was not there before

p_t Probability of capture (encounter) at day *t* given the individual has arrived but not yet departed

We used the Bayesian, state-space formulation of the JS model (Gimenez et al. 2007, Royle 2008), which contains one submodel for the state process (states are "not yet arrived", "present in the study area", "departed"), and another submodel for the observations encoded in the individual capture histories. The observation process is conditional on the current state. For each individual capture history h_i, there is a true state history accounted for by the vector z_i. This vector of binary state variables describes if an individual *i* is present, $z_{i,t} = 1$, or not, $z_{i,t} = 0$, in the stopover area on day *t*.

The state process is defined as:

$$z_{i,t}|z_{i,t-1} \sim Bernoulli\left(\phi_{t-1}z_{i,t-1} + \eta_t \prod_{j=1}^{t-1}(1 - z_{i,j})\right)$$

The term $\prod_{j=1}^{t-1}(1 - z_{i,j})$ is here to model the availability of the individual to enter in the stopover area and is equal to 1 when the individual has not yet entered the stopover area, and 0 when it has already entered.

As the binary observations are conditionally independent Bernoulli random variables, the link between the state and observation processes is given by the following equation:

$$h_{i,t}|z_{i,t} \sim Bernoulli(z_{i,t}, p_t)$$

This means that if an individual i has not yet entered the stopover area or has left it ($z_{i,t} = 0$), then $h_{i,t} = 0$ with probability equal to 1. If $z_{i,t} = 1$, then the capture history $h_{i,t}$ is a Bernoulli trial with probability p_t, which is the probability of capture at time t. This formulation allows us to estimate the time since arrival for each individual. This "time since arrival" covariate is a non-observable variable that can be computed with the sum of the true states $z_{i,t}$, which represents the presence of the individual i at time t at the stopover area:

$$TSA_{i,t} = \sum_{s=1}^{t-1} z_{i,s}$$

The state vector z_i. also allows us to use a new formulation of the stopover duration described in Lyons et al. (2016). We computed the mean stopover duration (in days) as follows:

$$SOD = \frac{\Sigma_i \Sigma_t z_{i,t}}{n}$$

where *n* is the number of individuals and *z* the true state variable (which defines if an individual was present or not at the stopover site on day *t)*.

To take into account the heterogeneity of detection probability between capture occasions and limit the number of parameters to estimate, we modeled detection probability (noted *p*) as a random process, instead of estimating a detection probability for each single day (capture occasion). Hence, we modeled *p* as,

$$logit(p) \sim Norm(logit\ (\mu_p), \sigma_p),$$

where μ_p, is the mean recapture probability and $\sigma_p$the standard deviation of the random effect.

The probability of remaining at the site was written as a function of all previously defined weather covariates and TSA, with a slope to be estimated for each covariate. When a slope had

a 95% credible interval excluding 0, the effect was considered statistically significant (Kéry and Schaub 2011). We analyzed the 20 years of data simultaneously, but accounted for potential differences between years (Péron et al. 2007) by means of a random year effect with *y* as the number of the year.

$$Year_y \sim Norm(\mu_{year}, \sigma_{year})$$

Experience (age) may also affect the decision of a bird to depart from a stopover site and thus affects stopover duration (Reilly and Reilly 2009, McKinnon et al. 2014, Vansteelant et al. 2017). To account for a potential effect of the experience, we also used age-dependent random effects (2 age classes: Adult or Juvenile with *a* as the age class) formulated as:

$$Age_a \sim Norm(\mu_{Age}, \sigma_{Age})$$

Using the logit link, the probability of staying at the stopover area between $t-1$ and t was formulated as:

$$Logit(\phi_{i,t-1}) = a + \beta_1 * TSA_{i,t-1} + \beta_2 * wind_{t-1} + \beta_3 * temperature_{t-1} + \beta_4 * cloudcover_{t-1} + \beta_5 * humidity_{t-1} + \beta_6 * \Delta\text{Pressure} + Year_y + Age_a$$

Because TSA is computed at each occasion for each individual, TSA cannot be standardized prior to the analyses. Hence, to compare the effect of TSA to the effects of weather covariates, we calculated the effect of a standardized TSA posterior to the analyses by multiplying the value of the TSA slope (β_1) by the standard deviation of all estimated TSA values.

Analyses were performed with JAGS (Hornik et al. 2003) using R. We used 60000 iterations, and we checked chain mixing and convergence (Kéry and Schaub 2011). The JAGS code is available in the Supplementary material.

3. Results

The mean estimated stopover duration for the whole study period was 12.5 ± 2.2 days [12.2; 12.8], with unstructured variation between years (Fig. 1). Adults (experienced birds) stay on average 1.6 days more than juveniles (naïve birds) (respectively, 13.8 ± 2.2 and 12.2 ± 2.1 days). This pattern (adults staying longer than juveniles) appears each year (Fig. 1). However, the 95% credible intervals and standard deviation of estimated stopover duration for juveniles and adults overlap (Fig. 1). Hence, more complex relationships between migratory experience and covariates were not explored.

The probability of staying at the stopover site between two occasions (ϕ_t, i.e. the complement of the probability of departing from the stopover site) was negatively related to the estimated individual time since arrival (TSA effect,

and Fig. 2). In other words, the longer a bird had already stayed at the site, the higher its probability to resume migration flight by the following night. The absolute value of the estimate for the effect of standardized TSA was the largest of all significant effects (Table 1). Hence TSA is the most important predictor of the probability of departing from the stopover site. TSA effect was also the most precisely estimated, suggesting a limited variability of TSA effect between individuals (see CI in Table 1).

Both humidity and ΔPressure had an effect on the probability of staying at the stopover site during the night (Table 1). The drier the conditions, the higher the probability that the bird resumes migration by the following night. In addition, the larger the increase in pressure between the two days before the night of departure, the higher the probability of leaving the stopover site. We did not find evidence for an effect of wind (Table 1). Cloud cover seemed to affect the probability of staying in the stopover area positively (Table 1), but the robustness of this interpretation is weak because one boundary of the CI overlaps 0. Plotting simultaneously

the respective effects of TSA and humidity (Fig 2a) or $\Delta pressure$ (Fig. 2b) illustrates that departure probability depends primarily on TSA, whereas the used weather covariates only have a moderate influence.

4. Discussion

4.1 Effect of the Time Since Arrival

The new way of statistical modeling the stop-over process hence revealed that the Time Since Arrival (TSA) is the major determinant of departure probability (at least in the studied species). This suggests that TSA could be a reliable indicator of how the propensity of the bird to leave the stopover site progresses through days, most likely because of the progressive change of its internal state. On the first day after arrival, birds are supposed to be exhausted, starving and with empty fuel stores. And the longer the TSA, the more they have had the opportunity to rest, feed and fatten.

As hypothesized, we believe that TSA is a good integrative proxy of the overall progress of the internal state of the stopovering bird and indicates different functions of stopover behavior: (i) the need for birds to rest after a migratory flight (McWilliams et al. 2004, Skrip et al. 2015), (ii) the need for birds to reach a sufficient level of fuel load to perform the following migratory flight (Schmaljohann and Eikenaar 2017) and (iii) the refueling rate which depends on the environmental conditions or physiological reactions involved in the refueling process. Here, TSA had a positive effect on departure decision: birds need to stay a sufficient number of days before leaving. For birds that do fatten, the fattening (or fuel deposition) increases through time: the longer a bird stops-over, the higher its last measured body mass or fuel load (mean mass gain of 0.48g in this study; T. Alerstam, 1990; Schmaljohann & Eikenaar, 2017) and the higher the daily mass gain (Péron et al. 2007). Starting from these points it may be reasonable to think that birds need a sufficient level of fuel store to perform another migratory flight (Alerstam

1990). Moreover, the resting time after a long migratory flight is apparently brief and confined to the first hours or days of the stopover (Fuchs et al. 2006, 2009, Németh 2009). This suggests that this is not the physiological process involving a 12 days stopover. Thus, most of the time spent in stopover is allocated to foraging to re-fill energy reserves, which is a long and progressive process that may be disturb by harsh weather. Hence, for the fraction of birds that do fatten and will perform a long-distance migratory flight from this stopover place, TSA may represent the physiological processes involved in refueling. Clearly establishing the link between TSA and fuel store is an important area of future research on stopover ecology.

Traditional measures of fuel store such as body mass or fat score may show some limitations (extensively discussed in Schmaljohann & Eikenaar, 2017; Schwilch & Jenni, 2001), of which we want to highlight two. (i) In many long-term migration monitoring programs of marked birds, especially in old datasets, weight was not systematically recorded at each recapture event. This drastically reduces the sample size available for long term analyses where we need a weight measurement at each recapture. In the French dataset for Sedge warblers, in the last century (before 2000), weight used to be taken for only 60% of capture events (Dehorter and CRBPO 2015). Nowadays (2000-2016 period), weight is taken for nearly all capture events (90%). (ii) Since the probability of being captured in a given day can be low in routine trapping protocols (0.161 [0.058, 0.376] in the present study; Schaub et al. 2001, Schmaljohann and Eikenaar 2017), the body mass measured at the latest capture is unlikely to be representative of the body mass that actually triggers departure. With a 0.161 capture probability per day, birds are rarely captured on the day of arrival, and on the night of departure. Imperfect detection probability is a common situation where modeling the bird history before the first capture is required to estimate arrival day. This imprecision in the assessment of the body mass progression through time could mask the effect of body mass on departure probability in dataset where daily capture probability is low. Apart from being the major driver of departure

probability, using TSA is a promising avenue in order to use past, long term capture recapture datasets and to avoid the bias induced by the non-availability of weight or fat score information at the very end of the bird's stay in the stopover area.

The relevance of TSA as a proxy of the internal state of the bird just before departure may be limited when birds stay only few days. In this case, birds may not improve condition with time spent at the stopover site because they may first continue to degrade upon arrival waiting for their digestive system to redevelop to refuel after a long-distant migratory flight (McWilliams et al. 2004). The relevance of TSA may also be limited when birds often relocate in the vicinity of the study site (Bächler and Schaub 2007) because the departure from the study site is not a departure to a long-distant migratory flight. Thus, birds do not need to improve their internal state to relocate few kilometers around. To get around these problems in capture-recapture datasets, birds captured only once are usually removed. It allows to remove most of the transients (Mills et al. 2011, Taylor et al. 2011, Sjöberg et al. 2015). Using TSA under such circumstances may even lead to erroneous conclusions about the stopover behavior of the focal species. We believe that integrating estimated TSA with fuel store data (body mass, fat score) could help to revisit previous analyses and to understand if the TSA effect represents the fuel store of the individual or other aspects of the internal state. It will help to understand the contrasted results of some studies about fuel store effects on departure probability (Tsvey et al. 2007, Schaub et al. 2008, Arizaga et al. 2011, Smith and McWilliams 2014, Schmaljohann and Eikenaar 2017).

4.2 Effect of weather conditions

In relatively humid days, birds tended to postpone departure. Birds wait for dryer conditions to resume their migratory flight. Humidity can be high even in absence of precipitation in Western Brittany. The negative effect of high humidity can reflect not only the inhibitory effect of rain, but also the increased flight cost when the air is very humid (Åkesson et al. 2001, Deppe et al.

2015). When atmospheric pressure increases between the day before the night of departure and two days before, the probability to depart from the stopover site increases. We hypothesize that, when birds perceive an increase in pressure (indicative of improving, anticyclonic conditions), this encourages them to resume migration flight by the following night. Unexpectedly, departure probability did not depend on wind, probably because wind was too rare and weak in the study area in August to be influential (mean wind force during the study period was 5 $m.s^{-1}$, see Supplementary material for a summary of the weather covariates). Based on our own results and previous studies (Lack 1960, Åkesson et al. 2001, Zehnder et al. 2001, Jenni and Schaub 2003, Schaub et al. 2004, Tsvey et al. 2007, Arizaga et al. 2011, Deppe et al. 2015, Sjöberg et al. 2015, Dossman et al. 2016, Vansteelant et al. 2017), the most influential weather covariates on departure probability are humidity, pressure and wind in areas exposed to substantial air mass movement during bird migration. Here we included all the covariates in the model despite a non-null collinearity between most of the environmental covariates (see Supplementary material for details). However, this collinearity appeared sufficiently low to allow the inclusion of all effects in a same model (Hair, Black, Babin, Anderson, & Tatham, 2006).

4.3 Effect of migratory experience

Juvenile birds (first migration) stay on average 1.6 days (11.6%) less than the older, more experienced birds at the stopover area. Even though there is no consensus about the age effect on migration strategy (Hake et al. 2003), this result is consistent with former studies that have shown that juvenile and experienced migrating birds behave differently: juveniles make shorter and more frequent stopovers (Reilly and Reilly 2009, McKinnon et al. 2014, Vansteelant et al. 2017). However, other studies reached opposite conclusions: telemetry studies of departure decisions in songbirds in the Gulf of Mexico did not find any effect of age on the decision to cross the Gulf of Mexico, or on the choice of weather conditions to cross the Gulf (McKinnon

et al. 2014, Deppe et al. 2015). Again, it is legitimate to ask whether imperfect detection probability is involved in inconsistencies among studies concerning the relationship between age and migration, because capture probability can vary with age (Rguibi-Idrissi et al. 2003, Pardo et al. 2013, Sanz–Aguilar et al. 2019).

4.4 Respective effects of TSA and weather conditions

The relative contributions of TSA *versus* weather conditions indicate that the TSA (a potential proxy of the overall progress of the internal state of the bird) is more determinant than weather conditions to depart from a stopover site for a long-distant migrant. This suggests that even in the presence of weather conditions favorable to departure, birds need to stay a certain amount of time before departing. As we do not know any studies on the relative contributions of the internal state versus meteorological conditions, we cannot directly compare this result to former studies. But, this result is consistent with numerous studies that highlighted the key role of the progress of the bird internal state (fuel store, fuel deposition rate, body condition, body mass, restness) on departure decisions from a stopover site (see Schmaljohann and Eikenaar (2017) for a review).

The progress of the internal state during a stopover may also be indirectly related to environmental conditions. Harsh weather may decrease the feeding ability and the food abundance in the stopover area. Thus, it will decrease the rate at which birds accumulate energy and affect the progress of the internal state of the bird (Jenni and Schaub 2003). Hence, weather conditions may affect TSA and thus stopover duration. However, even if global weather conditions during the stopover may affect stopover duration and the rate at which birds accumulate energy, birds still need to stay a certain amount time to fit with the energetic requirements for migration. This may indicate that the effect of TSA at time *t* on the departure probability at time *t* still be more determinant than weather conditions in the departure decision.

The relation between TSA and global weather conditions during the stopover is an area of future research to better understand the processes involved in departure decisions from a stopover site.

5. Conclusions

In this study, we integrated "Time Since Arrival" and weather conditions in a same analytical framework to disentangle the relative importance of each factor in the decision to depart from a stopover site. This allowed us to show that the TSA, a partially hidden individual state accessible with capture-recapture modeling, is a major determinant of departure decision (and thus of stopover duration), with a stronger effect than weather covariates, in a long-distant migrant songbird. This approach allows investigating the determinants of stopover duration and departure probability (not only weather variables but also some hidden physiological processes accounted for by TSA) in hundreds of existing long-term datasets, where there is no, or scattered information about mass or fat score. We demonstrated the feasibility and relevance of this analytical approach using data from one site, one species and over a large period of time. It will be necessary to use our modeling approach with data from several species, at several sites, to assess the robustness and generality of our conclusion about the major influence of TSA on the time when individuals decide to leave stopover sites.

TSA has also broader implications than just in migration ecology. For example, the movement of an individual between two foraging sites could also be dependent of a partially observable amount of time an individual has spent in the first site. Thus, TSA opens large perspectives when the triggering of a behavior depends on the time spent on a specific site, in a specific state or doing a specific activity.

Acknowledgements

This study was made possible thanks to tens of bird ringers and hundreds of assistants who volunteered in this long-term monitoring over three decades, and the continued support of Société d'Etude de la Protection et de la Nature de Bretagne / Bretagne Vivante, supervised by Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO), Museum National d'Histoire Naturelle, CNRS and Ministère de l'Environnement. All work was carried out in accordance with standard animal care protocols approved by the CRBPO. Emmanuelle Cam was supported by the French Laboratory of Excellence project "TULIP" (ANR-10-LABX-41; ANR-11-IDEX-0002-02).

References

Åkesson, S. and Hedenström, A. 2007. How Migrants Get There: Migratory Performance and Orientation. - Bioscience 57: 123–133.

Åkesson, S. et al. 2001. Reed warbler orientation: Initiation of nocturnal migratory flights in relation to visibility of celestial cues at dusk. - Anim. Behav. 61: 181–189.

Åkesson, S. et al. 2002. Nocturnal migratory flight initiation in reed warblers Acrocephalus scirpaceus: Effect of wind on orientation and timing of migration. - J. Avian Biol. 33: 349–357.

Alerstam, T. 1990. Bird migration. - Cambridge University Press.

Alerstam, T. 2011. Optimal bird migration revisited. - J. Ornithol. 152: 5–23.

Arizaga, J. et al. 2011. Effect of fuel load, date, rain and wind on departure decisions of a migratory passerine. - J. Ornithol. 152: 991–999.

B. Bargain et al. 2002. Importance des marais de la baie d'Audierne (Bretagne) pour la migration du phragmite des joncs Acrocephalus schoenobaenus. - Alauda 70: 37–55.

Bächler, E. and Schaub, M. 2007. the Effects of Permanent Local Emigration and Encounter Technique on Stopover Duration Estimates As Revealed By Telemetry and Mark-Recapture. - Condor 109: 142–154.

Baker, A. J. et al. 2004. Rapid population decline in red knots: Fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. - Proc. R. Soc. B Biol. Sci. 271: 875–882.

Becker, P. H. et al. 2008. Timing of initial arrival at the breeding site predicts age at first reproduction in a long-lived migratory bird. - Proc. Natl. Acad. Sci. U. S. A. 105: 12349–12352.

Bibby, C. J. and Green, R. E. 1981. Autumn migration strategies of Reed and Sedge Warblers. - Ornis Scand. 12: 1–12.

Crosbie, S. F. and Manly, B. F. J. 1985. Parsimonious Modelling of Capture-Mark-Recapture Studies. - Biometrics 41: 385.

Dehorter, O. and CRBPO 2015. Bird ringing and movement database for France. Centre de Recherches sur la Biologie des Populations d'Oiseaux, Muséum National d'Histoire Naturelle, Paris, France. http://crbpo.mnhn.fr/. Consulté le / Accessed on 21 August 2015. in press.

Deppe, J. L. et al. 2015. Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. - Proc. Natl. Acad. Sci. 112: E6331–E6338.

Dossman, B. C. et al. 2016. The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. - Behav. Ecol. 27: 567–574.

Fuchs, T. et al. 2006. Daytime naps in night-migrating birds: behavioural adaptation to seasonal sleep deprivation in the Swainson's thrush, Catharus ustulatus. - Anim. Behav. 72: 951–958.

Fuchs, T. et al. 2009. Daytime micro-naps in a nocturnal migrant: An EEG analysis. - Biol. Lett. 5: 77–80.

Gimenez, O. et al. 2007. State-space modelling of data on marked individuals. - Ecol. Modell. 206: 431–438.

Goymann, W. et al. 2010. Body fat influences departure from stopover sites in migratory birds: evidence from whole-island telemetry. - Biol. Lett. 6: 478–481.

Green, M. et al. 2002. Dark-bellied Brent Geese Branta bernicla bernicla, as recorded by satellite telemetry, do not minimize flight distance during spring migration. - Ibis (Lond. 1859). 144: 106–121.

Hahn, S. et al. 2009. The natural link between Europe and Africa - 2.1 billion birds on migration. - Oikos 118: 624–626.

Hair, J. F. et al. 2006. Multivariate data analysis (Vol. 6). in press.

Hake, M. et al. 2003. Age-dependent migration strategy in honey buzzards Pernis apivorus tracked by satellite. - Oikos 103: 385–396.

Hedenström, A. and Alerstam, T. 1997. Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. - J. Theor. Biol. 189: 227–234.

Hornik, K. et al. 2003. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling. in press.

Jenni, L. and Schaub, M. 2003. Behavioural and Physiological Reactions to Environmental Variation in Bird Migration: a Review. - Avian Migr.: 155–171.

Jolly, G. M. 1965. Explicit Estimates from Capture-Recapture Data with Both Death and Immigration-Stochastic Model. - Biometrika 52: 225.

Kéry, M. and Schaub, M. 2011. Bayesian Population Analysis using WinBUGS: A hierarchical perspective.: 1–554.

Ktitorov, P. et al. 2010. The good and the bad stopover: Behaviours of migrant reed warblers at two contrasting sites. - Behav. Ecol. Sociobiol. 64: 1135–1143.

Lack, D. 1960. The Influence of Weather on Passerine Migration. A Review. - Auk 77: 171–209.

Lyons, J. E. et al. 2016. Population size and stopover duration estimation using mark-resight data and Bayesian analysis of a superpopulation model. - Biometrics 72: 262–271.

Ma, Z. et al. 2011. Wind conditions affect stopover decisions and fuel stores of shorebirds migrating through the south Yellow Sea. - Ibis (Lond. 1859). 153: 755–767.

McKinnon, E. A. et al. 2014. Tracking from the tropics reveals behaviour of juvenile songbirds on their first spring migration (PA Bartell, Ed.). - PLoS One 9: e105605.

McWilliams, S. R. et al. 2004. Flying, fasting, and feeding in birds during migration: A nutritional and physiological ecology perspective. - J. Avian Biol. 35: 377–393.

Mills, A. M. et al. 2011. Passerines Use Nocturnal Flights for Landscape-Scale Movements

during Migration Stopover. - Condor 113: 597–607.

Németh, Z. 2009. Observation of Daytime Sleep-like Behavior in a Migratory Songbird during Stopover. - Wilson J. Ornithol. 121: 644–646.

Pardo, D. et al. 2013. Evidence for an age-dependent influence of environmental variations on a long-lived seabird's life-history traits. - Ecology 94: 208–220.

Péron, G. et al. 2007. Climate changes and post-nuptial migration strategy by two reedbed passerines. - Clim. Res. 35: 147–157.

Pledger, S. et al. 2008. Stopover Duration Analysis with Departure Probability Dependent on Unknown Time Since Arrival. - In: Modeling Demographic Processes in Marked Populations. pp. 349–363.

Prop, J. et al. 2003. Travel schedules to the high arctic: Barnacle geese trade-off the timing of migration with accumulation of fat deposits. - Oikos 103: 403–414.

Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall migration. - J. Anim. Ecol. 78: 990–1001.

Rguibi-Idrissi, H. et al. 2003. Variation in the stopover duration of Reed Warblers Acrocephalus scirpaceus in Morocco: Effects of season, age and site. - Ibis (Lond. 1859). 145: 650–656.

Royle, J. A. 2008. Modeling Individual Effects in the Cormack-Jolly-Seber Model: A State-Space Formulation. - Biometrics 64: 364–370.

Sanz–Aguilar, A. et al. 2019. Age–dependent capture–recapture models and unequal time intervals. - Anim. Biodivers. Conserv. 42: 91–98.

Sanz, J. J. et al. 2003. Climate change and fitness components of a migratory bird breeding in

the Mediterranean region. - Glob. Chang. Biol. 9: 461–472.

Schaub, M. et al. 2001. Migrating birds stop over longer than usually thought: An improved capture-recapture analysis. - Ecology 82: 852–859.

Schaub, M. et al. 2004. Departure of migrating European robins, Erithacus rubecula, from a stopover site in relation to wind and rain. - Anim. Behav. 67: 229–237.

Schaub, M. et al. 2008. Fuel stores, fuel accumulation, and the decision to depart from a migration stopover site. - Behav. Ecol. 19: 657–666.

Schmaljohann, H. and Eikenaar, C. 2017. How do energy stores and changes in these affect departure decisions by migratory birds? A critical view on stopover ecology studies and some future perspectives. - J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol. 203: 411–429.

Schmaljohann, H. et al. 2012. Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. - Anim. Behav. 84: 623–640.

Schwarz, C. J. and Arnason, A. N. 1996. A General Methodology for the Analysis of Capture-Recapture Experiments in Open Populations. - Biometrics 52: 860.

Schwilch, R. and Jenni, L. 2001. Low initial refueling rate at stopover sites: a methodological effect? - Auk 118: 698–708.

Schwilch, R. et al. 2002. Do migratory birds need a nap after a long non-stop flight? - Ardea 90: 149–154.

Seber, G. A. F. 1965. A Note on the Multiple-Recapture Census. - Biometrika 52: 249.

Sjöberg, S. et al. 2015. Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. - Anim. Behav. 104: 59–68.

Skrip, M. M. et al. 2015. Migrating songbirds on stopover prepare for, and recover from, oxidative challenges posed by long-distance flight. - Ecol. Evol. 5: 3198–3209.

Smith, A. D. and McWilliams, S. R. 2014. What to do when stopping over: Behavioral decisions of a migrating songbird during stopover are dictated by initial change in their body condition and mediated by key environmental conditions. - Behav. Ecol. 25: 1423–1435.

Taylor, P. D. et al. 2011. Landscape movements of migratory birds and bats reveal an expanded scale of stopover (T Mappes, Ed.). - PLoS One 6: e27054.

Tsvey, A. et al. 2007. Influence of body condition and weather on departures of first-year European robins, Erithacus rubecula, from an autumn migratory stopover site. - Behav. Ecol. Sociobiol. 61: 1665–1674.

Vansteelant, W. M. G. et al. 2017. Wind conditions and geography shape the first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan Africa. - Proc. R. Soc. B Biol. Sci. 284: 20170387.

Warnock, N. 2010. Stopping vs. staging: The difference between a hop and a jump. - J. Avian Biol. 41: 621–626.

Wikelski, M. et al. 2003. Costs of migration in free-flying songbirds. - Nature 423: 704–704.

Zehnder, S. et al. 2001. Nocturnal autumn bird migration at Falsterbo, South Sweden. - J. Avian Biol. 32: 239–248.

Figure 1: Between-year variation in individual stopover duration estimates (in days) per age category.

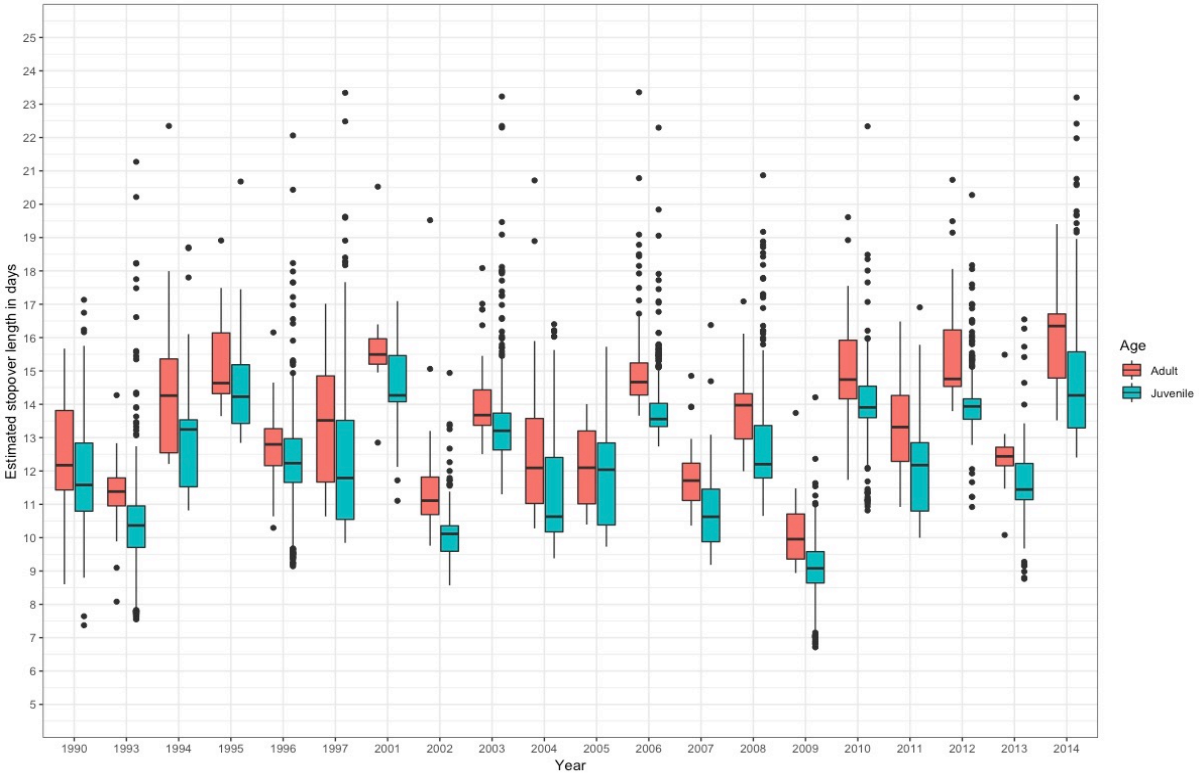

Figure 2: Departure probability as a function of the number of days since the bird arrived. (a) For different humidity conditions, dashed line: low humidity conditions (~70%); plain: high humidity conditions (~90%). (b) For different ΔPressure conditions, dashed line: a substantial decrease of atmospheric pressure (-5Hpa); plain: a substantial increase of atmospheric pressure (+5Hpa). The grey area represents departure probability values for humidity between 70 and 90% (a) and ΔPressure between -5Hpa and +5Hpa.

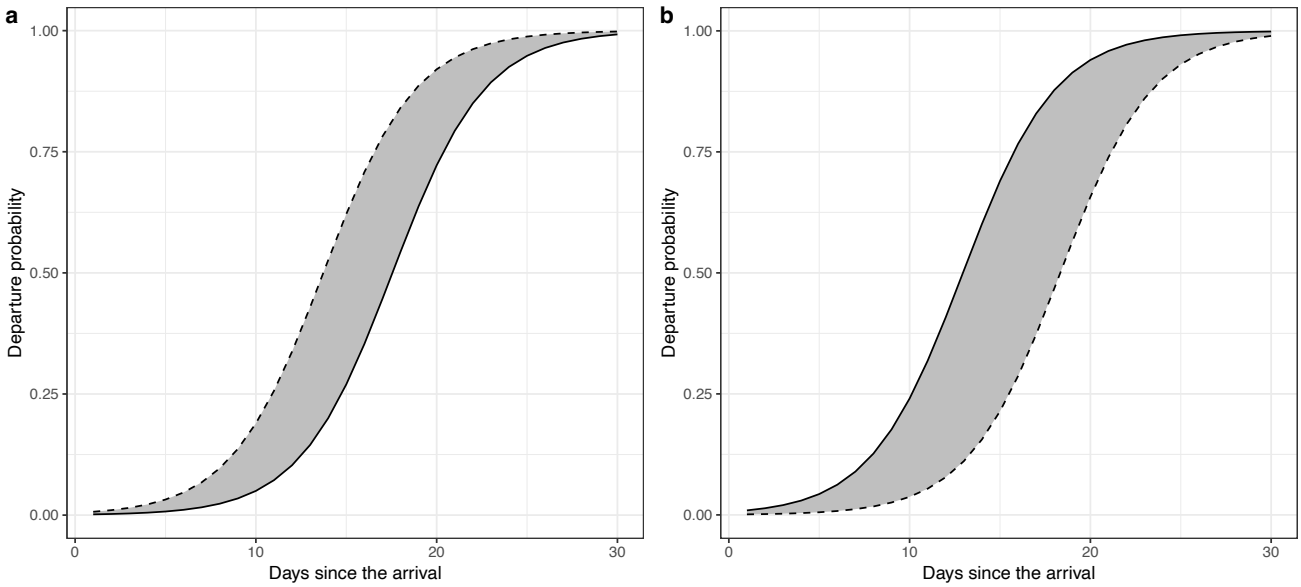

Table 1: Mean value, standard deviation and credible intervals (CI) for each covariate effect on the probability of staying at the stopover area. Bold: significant effects.

	Mean	*Sd*	*CI*
(a) Intercept	6.159	0.175	5.843, 6.578
(β_1) Time since arrival	**-1.538**	**0.039**	**-1.652, -1.432**
(β_2) Wind	0.116	0.1	-0.121, 0.196
(β_3)Temperature	-0.207	0.89	-0.387, 0.03
(β_4) Cloud cover	0.142	0.101	-0.052, 0.207
(β_5) Humidity	**0.497**	**0.121**	**0.261, 0.735**
(β_6) ΔPressure	**-0.702**	**0.23**	**-1.176, -0.196**