Hydrological management in a restored wetland affects stopover ecology of Aquatic Warbler: the case of La Nava wetland, northern Spain

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Abstract The Aquatic Warbler (Acrocephalus paludicola) is one of the most threatened migratory passerine birds in the world. The species stops over at both European and African wetlands during its migration. Using data from a long-term ringing program in the restored wetland of La Nava (Spain), we describe several aspects of the species’ stopover ecology at this site with special focus on juveniles: (1) timing of migration, (2) population size, (3) fuel reposition rate, (4) stopover duration and (5) site fidelity. We elaborated two Multiple Linear Regressions and a Generalized Linear Model to estimate the determinants of migration phenology, daily fattening rate and abundance of captures in addition to minimum observed stopover duration. Finally, we calculated return rates to estimate stopover site fidelity. We determined that: this stopover site belongs to an Atlantic migration route; juveniles experience delayed migration; and that reduced captures are associated with more restrictive hydrological management. Return rate results suggested that there is stopover site fidelity is low. Our results may indicate that this stopover site serves primarily as a resting place rather than a refuelling habitat for this species.

Key words Acrocephalus paludicola, Habitat fidelity, Migration phenology, Stopover duration, Wetland conservation

Stopover sites play an essential role in the survival of migratory bird species, as they are used for replenishing energy reserves, for resting, and for shelter (Newton 2004; Flade et al. 2011; Sheehy et al. 2011). It has been suggested that stopover sites may also play an important role in migration schedule adjustment (Peng et al. 2015). Wetlands are stopover sites of particular interest as they are both scarce and fragile (Green et al. 2002; Bellio & Kingsford 2013). Inadequate management of wetland habitats can result in a drastic reduction in their carrying capacity for threatened species, thus increasing mortality rates and the effects of inter- and/or intra-specific competition (Amezaga et al. 2002; Newton, 2004, 2006). Even so, few studies have investigated the effects of wetland habitat management on the conservation of migratory passerines (Poulin et al. 2002; Tanneberger et al. 2008), particularly in the Mediterranean basin (Bellio & Kingsford 2013) where degradation of wetlands reached 50% during the 20th century (>60% in Spain before 1990, Green et al. 2002). It is therefore essential to conduct in-depth studies into how the conservation of such stopover sites, and the species that select them, are being threatened.

The Aquatic Warbler (Acrocephalus paludicola Vieillot) is a long-distance migrant passerine catalogued as globally Vulnerable by the IUCN. Its nesting population is restricted to fragmented populations in wetlands in eastern Europe (Flade & Lachmann
E. J. MUÑOZ-ADALIA et al.

2008; Tanneberger et al. 2009) while its wintering grounds are located in western Africa (Cramp & Brooks 1992; Schäffer et al. 2006; Flade et al. 2011). Its population is estimated to have decreased by 90% during the 20th century (Tanneberger et al. 2009) mainly as a result of habitat degradation and changes in land use (Flade & Lachmann 2008; Arizaga et al. 2011b). Several aspects of its biology and ecology remain poorly known, particularly its migration phenology, the routes it follows and the characteristics of its stopover sites (Cramp & Brooks 1992; Schäffer et al. 2006; Arizaga et al. 2011b; Flade et al. 2011; Jiguet et al. 2011). Stopover habitats in the Iberian Peninsula are therefore of particular interest in view of the high level of degradation they have undergone (Mañosa et al. 2001; Moreno et al. 2007; Castañeda & Herrero 2008; Barba-Brioso et al. 2010; Hermoso et al. 2011) and their importance for the conservation of the species as they are the last fuel reposition sites before crossing the Mediterranean and the Sahara (Atienza et al. 2001; Salewski et al. 2013).

The aims of this study were to: (i) to improve our understanding of Aquatic Warbler migration phenology; (ii) analyse the stopover ecology of this threatened passerine; (iii) evaluate how hydrological management can affect stopover habitat quality, and finally (iv) investigate stopover site fidelity considering the special characteristics of Mediterranean wetlands.

We hypothesize that an adequately managed stopover site, with high water levels during the migratory period, will provide sufficient carrying capacity to shelter a large migrating population, and a short and effective stopover for refuelling, especially for juveniles. To the contrary, drier conditions will result in a lower carrying load of the ecosystem and low effectiveness of migration stopover. We hypothesize that migration phenology can vary depending on biological variables such as age, environmental parameters (including local weather and global meteorology), and time. Finally, fidelity to well-conserved stopover sites is expected to be high.

MATERIALS AND METHODS

1) Study area

The study area was La Nava wetland (Palencia, northern Spain. 42°3′50″N, 4°45′20″W. Fig. 1), a restored wetland that had almost completely dried out during the 1960s. In 1990, a restoration project was undertaken to recover 400 ha of the historically flooded 2,000 ha. Hydrological management of the wetland is currently aimed at imitating the natural cycles of winter flooding and summer drying. The water required for flooding is supplied in autumn and spring via a large hydraulic infrastructure named the Canal de Castilla; however, the volume of water transferred is not known as there are no annual records (Gómez 2006; Junta de Castilla y León 2010). The lagoon is classified as an Important Special Protection Area (Natura 2000), a Site of Community Importance (SCI) and a Ramsar Site.

Fig. 1. La Nava wetland location map. Protected areas in Castilla y León are shaded. Data: Junta de Castilla y León and Instituto Geográfico Nacional (http://www2.ign.es/iberpix/visoriberpix/visorign.html).
The area immediately surrounding the restored wetland is agricultural, and used for growing cereal crops and providing Mediterranean grassland for sheep grazing. A wide range of plants (e.g. Carex divisa Huds., Eleocharis palustris (L.) Roem. & Schult., Typha domingensis Pers. and Butomus umbellatus L.) and animals, particularly passerine birds (Acrocephalus spp., Motacilla spp., Passer spp., Sylvia spp., Luscinia spp., etc.), occurs in the wetland. La Nava wetland has a particularly high relevance for Aquatic Warbler as a stopover site during autumn migration (specific index value “Acrola” (Julliard et al. 2006): 5.29±1.36; Emigdio Jordán Muñoz-Adalia and Vittorio Baglione unpublished).

With regards food resource availability, Valladares et al. (1994) and Valladares and Garrido (2001), have reported strong seasonality in the macroinvertebrate community in La Nava and other neighbouring wetlands, in particular the abundance of aquatic beetles (Coleoptera; Adephaga and Polyphaga) is very low during summer (June-August). This suggests that the annual flood level may be a major constraint for prey populations, as generally occurs in Mediterranean wetlands (Waterkeyn et al. 2008).

2) Data collection

Between 2000 and 2008 we ringed Aquatic Warblers during 90 days each year starting the 15th of July. Mist-nets were opened daily for five hours from dawn onwards. We did not use play back of Aquatic Warbler territorial songs to lure birds because our special interest was in juvenile migrants. The number of mist-nets varied minimally between years (0–4 of 25 mist-nets) and the position of the mist-nets and their surroundings remained unchanged (Rodríguez et al. 2004).

The following data were obtained for each bird captured: date, type of capture (first capture or recapture between days), age (following Rodríguez et al.’s (2004) 1–9 scale, with 1 being a juvenile not yet able to fly and 9 four or more years old adult), wing length in millimetres according to Bairlein et al. (1995), and weight in grams measured with an electronic balance. The extent of body fat and muscles were estimated according to Bairlein et al. (1995). Body fat was measured according to 0–8 qualitative scale (0: bird without appreciable fat; 8: bird with the abdomen totally covered by fat). The extent of muscle development for each Aquatic Warbler was estimated using 0–3 qualitative scale (0: sternum sharp with muscles depressed; 3: sternum difficult to distinguish due to round muscles).

Data on climatic variables (accumulated rainfall during different periods and wind speed) were obtained from the Fuentes de Nava and Monzón de Campos weather stations (Palencia, Northern Spain) (http://www.jcyl.es/jcyl/cag/dgdr/riac/index.nn.html), both of which were located close to the study area. We also used monthly data from the North Atlantic Oscillation index (NAO) (http://www.cru.uea.ac.uk/~timo/datapages/naoi.htm). Data for defining the extent of hydrological management in the lagoon were also used, these described the monthly flooding level on a 1–4 scale (1: flooded wetland, depth of water 5–20 cm; 2: flooded wetland, depth of water 0–5 cm; 3: wetland with only surface humidity; 4: totally dry wetland) (Junta de Castilla y León unpublished).

3) Data analysis

All of the Multiple Linear Regressions (MLRs), Generalized Linear Models (GLMs) and ANOVAs used in the study were performed using R software (R Development Core Team 2011). Akaike’s information criteria (Anderson 2008) were used to select the definitive model in each case, choosing the most explicative model as it obtained a better corrected AIC value (AICc).

Migration phenology

An initial exploratory analysis of phenology was carried out by making an annual record of the date on which the maximum number of birds were captured, the median date of passage and also the dates of the earliest and latest captures (Atienza et al. 2001; Kozłowska et al. 2009).

A phenology model (MLR) was then constructed, in which the response variable was the Julian date on which each bird was first captured (FC) and the explanatory variables were study year and age, summer and annual rainfall and their possible interactions with biological meaning. Monthly NAO index values were added, as were those for the previous month, given that Zalakevicius et al. (2005) and MacMynowski and Root (2007) found a correlation between variations in these values and differences in dates of arrival on breeding grounds for long-distance migration passerine birds.

Population size and daily fattening rate

We ran a GLM with Poisson error and a log link function using the number of birds captured daily
as the response variable and year, sampling period expressed as fortnight (5th of July - 30th of September), management carried out in the wetland (on a scale of 1–4), rainfall accumulated in the fortnight and their interactions as explanatory variables. The monthly NAO value and that corresponding to the previous month were entered. The effect of the atmospheric conditions represented by this index on the migration phenology of passerine birds following both middle and long distance routes has already been documented (Zalakevicius et al. 2005; MacMynowski & Root 2007; Chambers et al. 2014), but has been little studied during autumn migration. The number of mist-nets located in the wetland each year was considered as an offset variable, to check for any possible effect of the variation in sampling intensity.

A daily fattening rate (E) was calculated for birds that were recaptured, and was a measure of weight in grams gained between capture and recapture divided by the minimum observed stopover duration (s) in days (see below). All of the rates and indices were calculated annually.

MLR was used to investigate the correlation between the daily fattening rate and the Julian date of first capture, year (Schaub & Jenni 2000) and Physical Condition index (CI; weight of bird in grams when captured, divided by wing length in millimetres (Winker 1995; Ktitorov et al. 2010). The model also included the amount of muscle and fat recorded at the time of capture and recapture (Bairlein et al. 1995), habitat management (on a scale of 1–4), mean annual and summer rainfall as well as during the minimum stopover period, stopover duration in days (s) and mean nocturnal and diurnal wind speed throughout the stopover period (Schaub 2004). All possible explanatory variables interactions were considered.

To control for a possible capture effect, we used ANOVA to analyse whether the fattening daily rate depended on stopover duration, categorized as “short” (≤3 days) and “long” (>3 days).

Stopover duration and site fidelity
Minimum observed stopover duration (s) was calculated as the number of days between the first capture and the last recapture of each bird (Rguiibri-Idrissi et al. 2003; Navedo et al. 2010). Two specific ANOVAs were calculated to analyse respectively the effect of management level (1–4 scale) and year on stopover duration.

In order to investigate stopover site fidelity, return rate (percentage of individuals recaptured in years following their first capture, compared to the total number of captures) (Nur et al. 1999) was calculated.

RESULTS

1) Migrant population size and migration phenology
A total of 683 captures were obtained (56.95% juveniles and 43.04% adults), 91 of which were recaptured (64.83% juveniles and 35.16% adults) (Table 1). During the study period, the maximum number of captures occurred each year between the 8th and the 24th of August, the median date of passage between the 14th and the 22nd of August, the earliest capture between the 17th of July and the 7th of August and the latest between the 12th and the 30th of Sep-

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Table 1. Number of captures, recaptures, daily fattening rate (E), minimum observed stopover duration (s) and return rate for Aquatic Warbler in La Nava wetland (2000–2008). Number of individuals in brackets expressed as (Juveniles/Adults). SE: Standard error.

<table>
<thead>
<tr>
<th>Year</th>
<th>Captures</th>
<th>Recaptures</th>
<th>E (g/day)±SE</th>
<th>s (days)±SE</th>
<th>Return rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2000</td>
<td>189 (126/63)</td>
<td>21 (18/ 3)</td>
<td>−0.03±0.09 (14/ 3)</td>
<td>4.96±1.69 (15/ 3)</td>
<td>−</td>
</tr>
<tr>
<td>2001</td>
<td>118 ( 70/48)</td>
<td>18 (14/ 4)</td>
<td>−0.03±0.13 ( 6/ 2)</td>
<td>3.07±1.26 (11/ 4)</td>
<td>2.54 (0/3)</td>
</tr>
<tr>
<td>2002</td>
<td>137 ( 75/62)</td>
<td>21 (11/10)</td>
<td>−0.15±0.10 ( 9/ 8)</td>
<td>3.45±1.30 (10/10)</td>
<td>1.46 (0/2)</td>
</tr>
<tr>
<td>2003</td>
<td>29 ( 15/14)</td>
<td>5 ( 2/ 3)</td>
<td>−0.28±0.10 ( 2/ 3)</td>
<td>1.83±1.83 ( 2/ 3)</td>
<td>3.45 (0/1)</td>
</tr>
<tr>
<td>2004</td>
<td>40 ( 9/31)</td>
<td>3 ( 1/ 2)</td>
<td>−0.13±0.03 ( 1/ 2)</td>
<td>2.50±1.50 ( 1/ 2)</td>
<td>2.50 (0/1)</td>
</tr>
<tr>
<td>2005</td>
<td>43 ( 21/22)</td>
<td>9 ( 5/ 4)</td>
<td>−0.14±0.16 ( 5/ 3)</td>
<td>6.63±2.77 ( 5/ 3)</td>
<td>4.65 (0/2)</td>
</tr>
<tr>
<td>2006</td>
<td>41 ( 21/20)</td>
<td>5 ( 3/ 2)</td>
<td>−0.34±0.32 ( 2/ 2)</td>
<td>1.50±1.00 ( 3/ 2)</td>
<td>0.00 (0/0)</td>
</tr>
<tr>
<td>2007</td>
<td>50 ( 33/17)</td>
<td>5 ( 2/ 3)</td>
<td>0.06±0.02 ( 2/ 2)</td>
<td>3.66±1.92 ( 2/ 3)</td>
<td>2.00 (0/1)</td>
</tr>
<tr>
<td>2008</td>
<td>36 ( 19/17)</td>
<td>4 ( 3/ 1)</td>
<td>−0.43±0.47 ( 3/ 1)</td>
<td>3.00±0.50 ( 3/ 1)</td>
<td>5.56 (0/2)</td>
</tr>
<tr>
<td>Mean±SE</td>
<td>75.88±7.86 (389/294)</td>
<td>10.11±2.54 (59/32)</td>
<td>−0.16±0.16 (44/26)</td>
<td>3.40±1.53 (52/31)</td>
<td>2.77±0.58 (0/12)</td>
</tr>
</tbody>
</table>
Aquatic Warbler stopover in La Nava wetland

The MLR corresponding to migration phenology (Table 2) showed a significant increasing delay in the first capture date during the study period. An unequal distribution of ages throughout the migration period was also observed; the date of first capture of adults occurred significantly earlier than that of juveniles. The model included the annual rainfall variable, although it was not significant. The first capture date was delayed as annual rainfall decreased. The remaining variables and interactions were not significant and did not improve the model’s AICc (Table 3).

Results obtained for the captures GLM showed no significant differences between management levels 1 (5–20 cm depth) and 2 (0–5 cm depth) (Table 2). However, the number of captures decreased significantly compared with reference level 1, for the most restrictive levels of management (3, surface humidity and 4, totally dry wetland). The number of birds captured was higher in all fortnights in comparison with the reference (15th–31th of July) (Table 2). The highest number of captures occurred during 16th–31th of August, followed by 1th–15th of August which, in turn, was higher than 1th–15th of September. During 16th–30th of September, the number of captures resulted higher than reference fortnight but no significantly. The remaining variables and interactions included were not significant and worsened the AICc value of the model (Table 3).


**Fig. 2.** Aquatic Warbler captures distribution by age and fortnights in La Nava wetland (2000–2008). Fortnights: a (15th–31th of July), b (1th–15th of August), c (16th–31th of August), d (1th–15th of September) and e (16th–30th of September). Sample size in brackets. SE: Standard error.

**Table 2.** Summary of phenology, captures and daily fattening rate models. $P_{\text{annual}}$: Annual rainfall, E: daily fattening rate, CI: Physical Condition Index, s: Minimum observed stopover duration, FC: First capture Julian date. Sample size in brackets. $^{*}$:z-value for Model Captures GLM. SE: Standard error.

<table>
<thead>
<tr>
<th>Model Phenology (n=707)</th>
<th>Estimate</th>
<th>SE</th>
<th>t$^*$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>$-1.02 \times 10^3$</td>
<td>$4.48 \times 10^2$</td>
<td>$-2.28$</td>
<td>0.02</td>
</tr>
<tr>
<td>Year</td>
<td>0.52</td>
<td>0.22</td>
<td>2.37</td>
<td>0.01</td>
</tr>
<tr>
<td>Age (Juveniles)</td>
<td>91.50</td>
<td>0.80</td>
<td>11.34</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>$P_{\text{annual}}$</td>
<td>$-9.02 \times 10^{-3}$</td>
<td>$6.07 \times 10^{-3}$</td>
<td>$-1.48$</td>
<td>0.13</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model Captures (n=54)</th>
<th>Estimate</th>
<th>SE</th>
<th>t$^*$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.89</td>
<td>0.22</td>
<td>8.48</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Management (0–5 cm)</td>
<td>$-0.62$</td>
<td>0.37</td>
<td>$-1.65$</td>
<td>0.09</td>
</tr>
<tr>
<td>Management (surface humidity)</td>
<td>$-1.93$</td>
<td>0.38</td>
<td>$-5.05$</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Management (Dry wetland)</td>
<td>$-2.14$</td>
<td>0.38</td>
<td>$-5.53$</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Forthnight (1th–15th August)</td>
<td>2.77</td>
<td>0.30</td>
<td>8.96</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Forthnight (16th–31th August)</td>
<td>3.05</td>
<td>0.30</td>
<td>9.94</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Forthnight (1th–15th September)</td>
<td>1.90</td>
<td>0.33</td>
<td>5.63</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Forthnight (16th–30th September)</td>
<td>0.54</td>
<td>0.41</td>
<td>1.30</td>
<td>0.19</td>
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</table>

<table>
<thead>
<tr>
<th>Model E (n=70)</th>
<th>Estimate</th>
<th>SE</th>
<th>t$^*$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.07</td>
<td>0.48</td>
<td>2.24</td>
<td>0.02</td>
</tr>
<tr>
<td>CI</td>
<td>$-8.74$</td>
<td>2.53</td>
<td>$-3.46$</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>s</td>
<td>0.03</td>
<td>0.01</td>
<td>2.96</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>FC</td>
<td>$6.00 \times 10^{-3}$</td>
<td>$3.00 \times 10^{-3}$</td>
<td>1.51</td>
<td>0.13</td>
</tr>
</tbody>
</table>
2) Stopover duration, refuel effectiveness and stopover site fidelity

The daily fattening rate was negative in all years except for 2007 (Table 1). Minimum observed stopover duration varied significantly neither in relation to the management level (ANOVA: F=0.50, P=0.67) nor the year (ANOVA: F=0.16, P=0.70). However, daily fattening rate increased significantly with the duration of the stopover (ANOVA: F=7.07, P<0.01).

The MLR for the daily fattening rate (Table 2) showed a significant decrease as the initial CI of the birds increased. The daily fattening rate showed an increase highly significant as the stopover period increased. The date of first capture showed a positive, though not significant correlation. This variable was included because it did not worsen the AICc of the model (Table 3). The remaining variables and interactions were not significant and neither did they improve the model’s AICc.

The calculated return rate was generally very low, and null during 2006 (Table 1).

DISCUSSION

1) Migration phenology

The migration phenology described for the species on possibly the most Atlantic route of the Aquatic Warbler (northern Spain and Portugal) (Robles & Arcas 2004; Miguélez et al. 2009; Neto et al. 2010; Arizaga et al. 2011a), follows a very similar phenological pattern to that obtained in our study. It is characterized by a marked increase in the migrating population during August, particularly in the second fortnight. The species was not seen after September, so birds captured from then on in other parts of the Iberian Peninsula (Atienza et al. 2001), are presumed to follow a route other than the Atlantic one (Mediterranean area and Ebro valley).

If we compare the phenology described in this study with that of European stopover sites, the highest migrating population density occurs in August also in Siena (Provost et al. 2010), Gironde (Musseau & Herrmann 2013) and the Bay of Audierne (Bargain 2009) in France, with a predominance of juveniles in the second fortnight. These coincidences in phenology, observed in stopover sites located in such dif-

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**Table 3.** Definitive model selection by AICc. P<sub>annual</sub>: Annual rainfall, P<sub>summer</sub>: Accumulated rainfall from June to August, Management: Management level applied in wetland (scale 1–4), NAO: Monthly North Atlantic Oscillation Index value (first capture month), NAO<sub>p</sub>: Monthly NAO value (first capture previous month), P<sub>fortnight</sub>: Accumulated rainfall in capture fortnight, Net: Annual number of mist-nets as offset factor, E: daily fattening rate, FC: First capture Julian date, CI: Physical Condition Index, s: Minimum observed stopover duration. Sample size in brackets. Selected model in boldface type.

<table>
<thead>
<tr>
<th>Model Phenology (n=707)</th>
<th>Model terms</th>
<th>Log Likelihood</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Year+Age</td>
<td>-2637.93</td>
<td>4</td>
<td>5283.91</td>
<td>0.00</td>
<td>0.53</td>
</tr>
<tr>
<td>2</td>
<td>Year+Age+P&lt;sub&gt;annual&lt;/sub&gt;</td>
<td>-2637.51</td>
<td>5</td>
<td>5285.12</td>
<td>1.20</td>
<td>0.29</td>
</tr>
<tr>
<td>3</td>
<td>Year+Age+P&lt;sub&gt;annual&lt;/sub&gt;+P&lt;sub&gt;summer&lt;/sub&gt;</td>
<td>-2637.29</td>
<td>6</td>
<td>5286.70</td>
<td>2.70</td>
<td>0.13</td>
</tr>
<tr>
<td>4</td>
<td>Year+Age+P&lt;sub&gt;annual&lt;/sub&gt;+P&lt;sub&gt;summer&lt;/sub&gt;+NAO</td>
<td>-2637.29</td>
<td>7</td>
<td>5288.74</td>
<td>4.82</td>
<td>0.05</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Model Captures (n=54)</th>
<th>Model terms</th>
<th>Log Likelihood</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Management+Fortnight</td>
<td>-135.78</td>
<td>9</td>
<td>293.66</td>
<td>2.56</td>
<td>0.22</td>
</tr>
<tr>
<td>2</td>
<td>Management+Fortnight+NAO</td>
<td>-420.95</td>
<td>10</td>
<td>867.02</td>
<td>575.91</td>
<td>0.00</td>
</tr>
<tr>
<td>3</td>
<td>Management+Fortnight+NAO&lt;sub&gt;p&lt;/sub&gt;+P&lt;sub&gt;fortnight&lt;/sub&gt;+Net</td>
<td>-555.72</td>
<td>8</td>
<td>1130.64</td>
<td>839.53</td>
<td>0.00</td>
</tr>
<tr>
<td>4</td>
<td>Management+Fortnight+Net</td>
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different latitudes, would support the classic theory that migration takes place in two different waves (Cramp & Brooks 1992), when mostly males, juveniles from the first clutches and some females migrate first and the remaining adults (mainly females) and last offspring born in the year do so in a second wave (Wojczulanis-Jakubas et al. 2013). As it is difficult to distinguish the sexes outside the breeding period, this aspect of the theory cannot be definitively corroborated, though our data support the two waves hypothesis.

As in our case, numerous studies have verified that adults migrate earlier than juveniles along the entire migration route (Robles & Arcas 2004; Miguélez et al. 2009; Neto et al. 2010; Arizaga et al. 2011a). The main explanation of this phenomenon may be that adults commence moulting when the females are still feeding their offspring. After that, whereas juveniles have to undergo dispersal and complete their body-moult, adults can start their migration to winter territories as in other Acrocephalus spp. (Chernetsov & Mukhin 2001; Mukhin et al. 2005; Tegetmeyer et al. 2012).

2) Hydrologic management effect in capture distribution

The GLM shows a negative correlation between the number of captures and the most restrictive levels of wetland management, which occurred from 2003 onward and which resulted in the lagoon drying out during July (Junta de Castilla y León unpublished). Such management of the ecosystem could have caused negative site selection, as the level of humidity was insufficient to guarantee adequate plant cover (shelter) and suitably abundant trophic resources (Poulin et al. 2002; Tanneberger et al. 2008, 2009; Gyurácz et al. 2011; Verkuil et al. 2012; Bellio & Kingsford 2013). This situation could have reduced the carrying capacity of the ecosystem, causing part of the migrating population to go elsewhere in search of more suitable habitat. Therefore, we propose a hydrological management system that will imitate the natural flooding-drying cycles of the La Nava wetland in order to maintain quality habitat and to guarantee a better stopover site for this and other species.

Regarding the NAO index, Zalakevicius et al. (2005) suggested that its effect is felt less intensely by long-distance migrants than in species that move over shorter distances. Our results support this view, being NAO excluded from the best model of number of captures.

3) Stopover duration and refuel effectiveness

The minimum observed stopover duration calculated for Aquatic Warblers at La Nava were lower than those estimated for other Iberian (Miguélez et al. 2009) and French (Musseau & Herrmann 2013) wetlands. However, our estimate is slightly higher than that calculated by Bargain (2009) for northwest France. The results suggest great heterogeneity between locations, even between sites that are relatively close together.

No differences in minimum observed stopover duration according to year or management level were found. However, low recapture rate may have limited the power of the analyses and hindered the use of more complex models that included demographic factors, such as mortality or presence of transient individuals, that would have improved the estimation of stopover duration.

The MLR showed that CI had a significant effect on the daily fattening rate, thus birds that arrived in worst physical conditions lost less weight during stopover. This relationship was not found by Rguibi-Idrissi et al. (2003) for the Reed Warbler (Acrocephalus scirpaceus Herman). We also found that a longer minimum observed stopover duration was correlated with higher fattening rates. This may be due to a “capture effect”, which hindered fattening during the first days after being ringed, as suggested by Salewski et al. (2007).

However, Ktitov et al. (2010) indicated that birds tend to leave earlier stopover sites that are not adequate for fuel reposition, and use them only for resting (Arizaga et al. 2011b). Therefore, it may be also possible that a low fattening rate forced some Aquatic Warblers to leave earlier, producing the pattern observed. At present, it is therefore difficult to disentangle a capture effect from a defective state of the wetland during migration. Further studies are needed to evaluate the availability and abundance of trophic resources in this stopover site.

4) Aquatic Warbler stopover site fidelity

This species showed little fidelity to La Nava wetland (mean return rate=2.77%). However, estimating site fidelity considering only return rate can be conservative, because of other implied factors (e.g. mortality). Catry et al. (2004) also reported that long-distance migrating passerines demonstrated low fidelity to their stopover sites (estimated maximum return rate 12.9—26.2% for A. scirpaceus in Portugal according to these authors). Such low fidelity could
be because the energy invested in re-visiting the same sites is not compensated for in terms of fuel reposition, not even in such scarce and dispersed habitats as wetlands. Interannual oscillations in water and food availability, characteristic of La Nava as a Mediterranean wetland (Tanneberger et al. 2009; Bellio & Kingsford 2013), could lead to uncertainty with regard to replenishing fat reserves, which would account for the low site fidelity observed.

5) Stopover sites as key in threatened migratory bird conservation.

Our results show that inadequate wetland management can drastically reduce the carrying capacity of the ecosystem. Reduced stopover effectiveness during migration, owing to a loss in habitat quality, can represent a major threat for migrating birds, especially endangered species such as the Aquatic Warbler.

It is therefore necessary to conduct further in-depth studies into the effects of human management on factors (such as: availability of prey, existing shelters, inter- and intra-specific competition) that determine the quality of stopover sites in order to establish effective conservation strategies. Also, factors influencing migration, from local ground use to climatic impacts on a global level, must be investigated.

ACKNOWLEDGMENTS

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Cramp S & Brooks DJ (1992) Handbook of the birds of Europe the Middle East and North Africa: the birds

REFERENCES


for Statistical Computing, Vienna.


