How many Aquatic Warblers Acrocephalus paludicola stop over in France during the autumn migration?

Frédéric JIGUET1*, François CHIRON1, Olivier DEHORTER1, Hubert DUGUÉ2, Pascal PROVOST3, Raphaël MUSSEAU4, Gaëtan GUYOT5, Franck LATRAUBE6, Philippe FONTANILLES7, Emmanuel SÉCHET8, Julien LAIGNEL9, Xavier GRIWIER10 & Arnaud LE NEVÉ5

1UMR 7204 MNHN-CNRS-UPMC, Centre de Recherches sur la Biologie des Populations d'Oiseaux, CP 51, 55 Rue Buffon, 75005 Paris, FRANCE
2Association ACROLA, La Jannais des Douets, 44360 Cordemais, FRANCE
3Maison de l’Estuaire, RNN Estuaire de Seine, 20 rue Jean Caurret, 76600 Le Havre, FRANCE
4BioSphère Environnement, 52 quai de l’Estuaire, 17120 Montagne-sur-Gironde, FRANCE
5Bretagne Vivante SEPNB, 186 rue Anatole France, B.P. 63121, 29231 Brest cedex 3, FRANCE
6Réserve du Massereau, Station ONCFS, Les Champs Neufs, 44320 Frossay, FRANCE
7Observatoire d’Intérêt Ornithologique, Cami deth Sailhetou, 65400 Lau Balagnas, FRANCE
820 rue de la Résistance, 49125 Cheffes, FRANCE
9Cap Ornis Baguage, 10 rue de la Maladrerie, 59181 Steenwerck, FRANCE
10Maison du garde, Les Escardines, 62215 Oye plage, FRANCE
*Corresponding author, e-mail: fjiguet@mnhn.fr


Abstract. The autumn world population of the endangered Aquatic Warbler Acrocephalus paludicola probably numbers between 23,000 and 69,000 individuals, including 5,000 to 44,000 first-year individuals, depending on variation in breeding success and post-fledging survival. After breeding, the species migrates as early as August along a westerly route along French coast to reach its African wintering grounds. In 2009, French ringers have carried out targeted mist-netting to enhance the capture of the species, using tape luring in suitable habitats. Overall, 874 different individuals were captured in France in that year. In 2010 similar ringing effort allowed the capture of 646 different individuals. From this ringing information, we propose a simple method to estimate the number of individuals which stopped in the country during the autumn migration, considering all birds or first-years only. Splitting the country in two parts (northern and southern), the method uses the total number of captures and the number of southern recaptures of birds first ringed in the north. Overall, we estimated that between 24,000 and 30,000 individuals — most of them in their first calendar year — stop in France each year during the fall migration. These estimates suggest that probably all first-year Aquatic Warblers migrate by this western flyway and stop in France to refuel, while adults may partly use a different flyway or may stop in France, but for shorter times or at fewer sites. The proposed figures highlight the importance of maintaining suitable refuelling habitats for the species all along coastal France.

Key words: Acrocephalus paludicola, capture effort, recaptures, refuel, ringing, stopover

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INTRODUCTION

The Aquatic Warbler Acrocephalus paludicola is the most threatened European migratory songbird (BirdLife International 2010). Its population has declined dramatically over the last decades, largely because of the drainage of its wetland breeding habitats. Most Aquatic Warblers use a western migration route in autumn (Dyrcz 1992), with large numbers visiting French coastal marshes mainly in August, where many important stopover sites have been identified (Julliard et al. 2006). In 2009, French ringers were invited to follow a standardized protocol dedicated to maximize captures of the species, using tape luring in suitable habitats. Classical extensive warbler ring-
ing in reedbed habitats (see e.g. Péron et al. 2007) provided further captures of Aquatic Warblers. Overall, 874 individuals were ringed in France at 44 different sites in 2009. In summer 2010, 646 different individuals were similarly captured at 43 different ringing sites.

There are no published estimates of the global post-breeding population size for the Aquatic Warbler. However, the estimate of singing males is 9 700–13 300 (figures published by Flade & Lachmann 2008, updated with information published in Malashevich 2010 and at http://www.aquaticwarbler.net/sar/), so if the balanced offspring sex-ratio (Dyrcz et al. 2004) is maintained at maturity, breeding counts would include 19 400–26 600 mature individuals. However, breeding populations show a male surplus (54% of males, Giessing 2002) so that the species probably numbers between 18 000 and 24 600 mature individuals, including approximately 8 300–11 300 females. The breeding success has been estimated to be 2.5 to 3.4 fledglings per successful nest but can be very variable between sites and years (Dyrcz & Zdunek 1993a, Schulze-Hagen et al. 1989, 1999, Dyrcz et al. 2005, Vergeichik & Kozulin 2006). Moreover, part of the females do breed twice a year (depending on habitat, probably at least 30%; see Dyrcz & Zdunek 1993b), while the true frequency of second clutch is not well known. To better account for all these parameters potentially affecting estimates of the post-breeding population size in the Aquatic Warbler, we will consider a few scenarios based on various reported rates of successful brood and number of fledglings per successful brood, according to Dyrcz & Zdunek (1993b) and Vergeichik & Kozulin (2006). We thus obtained four different scenarios for estimates of the number of juveniles per adult female after the breeding season, used to obtain estimates of the potential global number of juveniles and therefore individuals migrating in summer and autumn. These estimates provide an upper and a lower limit, which however do not consider any post-fledging mortality before departure on migration.

METHODS

Estimates of the post-breeding population size
To obtain estimates of the number of juveniles after the breeding season, we first considered simple rules for breeding decisions by females: all females lay at least a brood, and an average 30% of females lay a second brood (the first being either successful or not). We then applied the reported values of the number of fledglings per successful nest as reported in Dyrcz & Zdunek (1993b) for Biebrza marshes in NE Poland (62.7% of successful nests, 4.4 and 3.3 fledglings per successful nest for first and second brood, respectively), and Vergeichik & Kozulin (2006) for Belarussian marshlands: Dikoe (18.5% of successful nests, 2.5 fledglings per successful nest), Zvanets (42.3% of successful nests, 3.4 fledglings per successful nest) and Sporovo (10.4% of successful nests, 3.2 fledglings per successful nest). We then used the formula:

\[ N_{juv} = N_f \times (sn_1 \times juv_1 + 0.3 \times sn_2 \times juv_2) \]

where \( N_f \) is the total number of adult females (8 300–11 300), \( sn_1 \) and \( sn_2 \) are the proportions of successful nest for the first and second brood respectively (\( sn_1 = sn_2 \) for Dikoe, Zvanets and Sporovo), \( juv_1 \) and \( juv_2 \) the number of fledglings per successful nest.

Ringing protocols in France
In 2009, the French ringing centre established a special ringing protocol dedicated to the capture of migrating Aquatic Warblers. Ringers are invited to place a ringing unit comprising a line of mist-nets 36 meters long, with a tape playing the song of the species at the middle of the line. Playback starts at dawn, and ringing activities stop at noon.
The protocol recommends that the ringing units are placed at the interface between reedbed and wet grassland or mixed areas, as habitat is used by the species to refuel (Provost et al. 2010). Details of the protocol can be downloaded at http://www2.mnhn.fr/crbpo/IMG/pdf/THEME_ACROLA-2.pdf. This method has proved very efficient for attracting and capturing Aquatic Warblers during the autumn migration (Julliard et al. 2006), and has allowed the capture and ringing of 530 individuals in 2009 (450 first-year; 80 adult birds; age-ratio 0.85). Ringing activities are also common in reedbed habitats in France in August and September, with extensive ringing of reed warblers Acrocephalus sp., which adds to the available information on captured and ringed and distantly recaptured Aquatic Warblers. Overall, 874 Aquatic Warblers have been captured in France in summer 2009, including 759 first-year and 115 adults. In summer 2010, 646 different individuals have been captured, including 531 first-year and 115 adults. 22 birds in 2009, respectively 14 in 2010, ringed in France have been further recaptured the same year at a different site in the country, providing more information on migration timing and strategy.

For population size estimates, we only used data of birds ringed and recaptured in the same year, and considered birds ringed in the previous years and recaptured in France in the study year as if they were ‘unringed’ when first captured in France in the study year (concerns 4 adults in 2009 and 3 in 2010).

### Splitting France to estimate migrant numbers

Ringing data came from 44 different ringing sites in 2009 (Fig. 1) and 43 sites in 2010 (with approximately a similar spatial distribution). To estimate how many migrants stop in France, we split the country in two parts, separating a northern coast line and a more southern one. We performed three different splits along the French coastline to test the robustness of further calculations (Fig. 1).

- A first cut separated coastal departments north and south the limit between Normandy and Brittany (48°38’N, 1°35’W), a second split separated sites north and south of the administrative limit between Morbihan and Loire-Atlantique (47°27’N, 2°28’W), a third split separated sites north and south of the administrative limit between departments of Loire-Atlantique and Vendée (at 47°01’N, 1°59’W). These splits intended to separate France in two parts where Aquatic Warblers could conceivably stop while migrating.

### Method to obtain estimates

The method focuses on birds captured in the southern part of the country. Birds entering the southern part are either unringed (not captured in the north) or already ringed (captured in the north), and all have the same probability of being captured in the south. This assumes that all birds stopped somewhere in the north, and have the same probability of being captured in the south. It also supposes the absence of any trap-shyness or trap-happiness (changing avoidance or attraction to mist-nets after a first capture). The proportion of birds not captured in northern sites then captured in southern sites should equal the proportion of birds captured in the north then recaptured in the south. So we have the equation:

\[
\frac{n_{RS}}{(N - n_{RN})} = \frac{n_{CS}}{n_{RN}}
\]

where \( N \) is the total number of individual stopping in France, \( n_{RN} \) is the number of individuals captured and ringed in the north, \( n_{RS} \) is the number of individuals captured and ringed in the south, and \( n_{CS} \) is the number of individuals captured and ringed in the north and recaptured in the south. This equation leads to the following estimate of the total population:

\[
N = \frac{n_{RN} \cdot (n_{RS} + n_{CS})}{n_{CS}}
\]

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Fig. 1. Sites where Aquatic Warblers have been ringed in France during the 2009 fall migration (open circles). The geographic splits are reported, showing the three ways of delimiting a northern and a southern ringing datasets (namely split 1, split 2 and split 3). Administrative departments with data used in this study are coloured along a grey scale depending on their position along the splits.
We performed this formula considering $n_{RN}$ as the number of birds ringed north of the splitting limit first in France only, then by completing the dataset (northern ringing and southern recaptures) with birds ringed in Belgium (2009: $n = 72$, including 51 first-year; 2010: $n = 52$, including 34 first-year, 11 adults and 7 of unknown age) and in the Netherlands (2009: $n = 25$, including 24 first-year; 2010: $n = 15$, including 13 first-year) too. One adult bird ringed in 2009 in Belgium (Neerpelt in Limburg) was further controlled in France (at Grand Lieu in Loire-Atlantique) the same year. One first-year bird ringed in 2009 in the Netherlands was further controlled in France the same year (at Donges, Loire-Atlantique).

Note that this method is robust to eventual differences in capture probability between the northern and southern parts of the study area, because it just assumes that a ringed and an unringed individual have the same capture probability in the southern part.

**Confidence intervals**

For each split, we calculated confidence intervals of estimated population sizes based on the Poisson error distribution of $n_{CR}$, because error of this parameter varies the most when estimating total migrating population. Upper and lower confidence values of this parameter were further introduced in the equation to obtain the upper and lower limits of the confidence intervals.

### RESULTS

**Estimates of post-breeding population size**

Applying the demographic rates reported in the methods, we obtained four estimates of the potential number of juveniles after the breeding season (estimates rounded to the nearest 10 figure): (1) 32,530–44,290 (Biebrza); (2) 7,180–9,780 (Dikoe); (3) 20,340–27,690 (Zvanets); (4) 5,320–7,250 (Sporovo). From these figures, we propose to further consider that the post-fledging number of juvenile Aquatic Warbler should range between 5,300 and 44,300 individuals, so that the total post-breeding world population probably number 23,300–68,900 individuals.

**Estimates of migrant numbers stopping in France**

For each year, we applied the method using each of the three splits of the country, and for all individuals but also for first-year birds separately. Overall, we estimated that between 24,000 and 30,000 individuals — most of them in their first calendar year — stop in France each year during the fall migration. Detailed estimates of the number of Aquatic Warblers stopping in France in 2009 and 2010 are presented in Table 1. For each year, the bottom row reports the mean estimate and the associated standard error obtained for the three spatial splits. In 2009, the estimates obtained with split 3 for all birds is smaller than for first-years only; the reason is the large influence of the variation in the number of ringed adults recovered in the south on the estimates.

#### Table 1. Estimates of the total number of Aquatic Warblers stopping in France during the autumn migration in 2009 and 2010, obtained with three ways of splitting the country into a northern and a southern part, and when considering all captured birds, or only first-year individuals. Averages ± standard errors are given when considering or not Belgian and Dutch ringing data. Estimates have been rounded to the nearest 10 figure.

<table>
<thead>
<tr>
<th>Data</th>
<th>Split</th>
<th>All birds</th>
<th>CI (lower-upper)</th>
<th>First-year</th>
<th>CI (lower-upper)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>16 690</td>
<td>9 475–33 100</td>
<td>13 900</td>
<td>7 690–28 670</td>
</tr>
<tr>
<td>French</td>
<td>2</td>
<td>21 660</td>
<td>11 620–46 840</td>
<td>18 420</td>
<td>9 540–42 150</td>
</tr>
<tr>
<td>2009</td>
<td>3</td>
<td>39 880</td>
<td>14 110–190 730</td>
<td>43 300</td>
<td>10 360–138 620</td>
</tr>
<tr>
<td>Mean ± s.d.</td>
<td>26 080 ± 12 210</td>
<td>25 210 ± 15 830</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>French</td>
<td>1</td>
<td>19 810</td>
<td>11 500–39 240</td>
<td>17 510</td>
<td>9 690–36 110</td>
</tr>
<tr>
<td>Belgian</td>
<td>2</td>
<td>23 860</td>
<td>13 220–49 180</td>
<td>21 940</td>
<td>11 360–50 190</td>
</tr>
<tr>
<td>Dutch</td>
<td>3</td>
<td>45 350</td>
<td>16 050–216 860</td>
<td>48 510</td>
<td>11 600–155 310</td>
</tr>
<tr>
<td>2009 Mean ± s.d.</td>
<td>29 670 ± 13 730</td>
<td>29 320 ± 16 770</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>French</td>
<td>1</td>
<td>17 010</td>
<td>7 390–52 020</td>
<td>14 900</td>
<td>5 940–53 730</td>
</tr>
<tr>
<td>2010</td>
<td>2</td>
<td>23 810</td>
<td>9 470–85 980</td>
<td>16 720</td>
<td>6 680–60 260</td>
</tr>
<tr>
<td>3</td>
<td>31 480</td>
<td>9 100–256 290</td>
<td>20 810</td>
<td>6 080–168 760</td>
<td></td>
</tr>
<tr>
<td>Mean ± s.d.</td>
<td>24 100 ± 7 240</td>
<td>17 470 ± 3 030</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>French</td>
<td>1</td>
<td>23 310</td>
<td>10 130–71 280</td>
<td>19 320</td>
<td>7 700–69 720</td>
</tr>
<tr>
<td>Belgian</td>
<td>2</td>
<td>30 960</td>
<td>12 320–111 810</td>
<td>20 660</td>
<td>8 250–74 490</td>
</tr>
<tr>
<td>Dutch</td>
<td>3</td>
<td>35 460</td>
<td>10 250–288 740</td>
<td>23 040</td>
<td>6 730–186 870</td>
</tr>
<tr>
<td>2010 Mean ± s.d.</td>
<td>29 910 ± 6 140</td>
<td>21 010 ± 1 880</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
as an increase \( n_{CS} \) has a strong effect on the estimates.

**DISCUSSION**

Using the complete dataset of Aquatic Warblers captured in France in 2009, we estimated that at least 16 690, and more probably between ca. 26 000 to 30 000 birds stopped in northern and in southern France to refuel (range 16 700–45 350 individuals). Estimates obtained from ringing data for 2010 were very similar, with at least 17 010, probably between 24 000 and 30 000 birds. Most of these are first-year individuals, which confirms that the known world population of this endangered species migrates along a western route and uses French wetlands to rest and refuel. This is also supported by ring recoveries within the post-breeding French migrants. Some birds ringed on breeding grounds have been captured while stopping in France, with individuals from Polish Pomerania (Karsiborska Kępa, Zachodnio-Pomorskie, 53°52', E14°15'E), eastern Poland (Łomża, Podlaskie, 53°20'N, 22°40'E) and Belarus (Dikoye fen mire, 52°50'N, 24°20'E). Four migrants ringed in France have been further captured on breeding grounds, in Poland (Husynne, Lubelskie, 51°08'N, 23°50'E) and in Ukraine (Supoi, 50°40'N, 31°35'E). The estimates of the population stopping in France are larger than the current estimates (5 000 to 15 000) of the population wintering at the known Senegalese wintering site (Salewski et al. 2009), while two individuals among the 55 ringed in January 2009 in the Djoudj (Flade et al. 2011) have been recaptured during the fall migration in France in August 2009.

Because the method relies on recapture events and is highly dependent on the amount of available data, recapture events are most important in limiting the available information. Analysing data in the forthcoming years will provide larger dataset to further test the robustness and repeatability of the estimates. The amount of available data certainly influences the precision of the estimates. Indeed, the smallest coefficient of variation (standard error divided by mean) was obtained when maximizing the amount of data used in calculations, i.e. when considering all individuals (from the three countries, of both age classes, and obtained whatever the ringing protocol), resulting in an estimate for the stopover population of ca. 20 000 to 45 000 individuals. Overall, the validity of the estimates depends also on the validity of some assumptions. The method assumes the absence of any trap shyness or trap attractiveness for birds already captured once. As we consider only inter-sites recaptures, this assumption is very probably met. The method assumes that all birds stop in the northern and the southern parts of the country. This is probably the case if the Aquatic Warbler uses the same refuelling strategy as other Acrocephalus warblers migrating through Western Europe (Bibby & Green 1981), but we can not exclude a possibility that some birds only stop once in France. For example, we could expect that birds which stopped in the north have a lower probability of being captured again in the south, either because they do not stop again or because they stop for shorter times (they already partly refuel). In such cases, the obtained estimates would be overestimates. That is very probably the reason of the very large estimates obtained with split 3, the one with the most southern demarcation line. Indeed, this split places the Seine and the Loire estuaries, probably the two most important stopover sites, in the same split part. However, the age-ratio of the estimates suggests that the true number of Aquatic Warblers migrating and refuelling in France is larger than the proposed figures. Indeed, the age-ratio of the captures is not equal to the expected post-breeding age-ratio (2 juveniles for 2 adults). Nevertheless, the age-ratio during the post-breeding migration is probably lower because of juvenile mortality between ringing at the nest and migration stopovers. The average age-ratio of birds ringed in France is 0.88 in 2009 (88% of first-year birds), and the average age-ratio of the estimates is 0.83 or 0.85 (using split 1 and 2, respectively). Adult birds might use a different migration route, though the most plausible explanation is that they have a lower capture probability than first-year birds, either because they are less attracted to tape luring or because they have a different migration stopover system — they might stop for shorter times and less frequently as they are probably more efficient to refuel while on stopover. If they stop fewer times, they could also stop only in the northern or in the southern part considered here. When considering the figures obtained for first-year birds, we can conclude that probably all or at least a very large fraction of birds hatched in a year (5 300–44 300) do migrate and stop along French coasts (17 000–48 000 in 2009, 19 000–23 000 in 2010). Confidence intervals were particularly large, and from the obtained values we can only conclude that at least 7 700 individuals do stop in
France, while the upper limits are all larger than the world population size.

The Aquatic Warbler is the most threatened European migratory songbird, while the vital importance of migration stopover sites to en route songbirds has come to the forefront of avian conservation (Huutto 1998, Petit 2000). French wetlands are therefore of primary importance for these migrants to rest and deposit fat reserves at stopover sites while travelling from the breeding to the wintering grounds. The spring migration might occur on a larger front in the Mediterranean basin, though recent captures seem to indicate that southern France might provide important spring stopover sites too (Poulin et al. 2010). From various evidence, the Aquatic Warbler appears to use wet grassland and not reedbeds as foraging habitats to breed (Tanneberger et al. 2010), refuel on migration (Bargain 2002, Provost et al. 2010) and winter (Salewski et al. 2009, Flade et al. 2011). Wet grasslands at stopover sites are however only small distantly-connected habitat patches, while breeding or wintering habitats cover thousands of hectares in flooding plains — hence the need to care for their maintenance, distribution and connectivity. The identification of high-priority stopover sites and of stopover habitats critical to the long-term persistence of the migratory strategy is necessary to implement comprehensive conservation schemes (Yong et al. 1998, Petit 2000). France therefore has a large responsibility to protect, manage and even create suitable autumn stopover habitats for the migrant Aquatic Warblers to forage and refuel on their way to their African winter grounds.

In this study, we proposed a simple method based on ringed and recaptured ringed birds to estimate the size of a population stopping during migration. This method assumes that the proportion of individuals ringed north of an arbitrary limit and recaptured south of this limit is equal to the proportion of birds not captured in the north but captured and ringed in the south. It does not need to estimate the capture or recapture effort, and could be applied to ringing data gathered at large spatial scale, for example for estimating the migrant population sizes of passerines, especially for species of conservation concern. This is the case for Skylarks *Alauda arvensis*, hunted in southern France during the autumn migration, in order to estimate possible temporal trends in the number of migrants, and the opportunity to continue hunting a species which breeding numbers are declining in Europe (Gregory et al. 2005). The method could also be used to estimate the number of migrant Ortolan Buntings *Emberiza hortulana* using a western flyway and susceptible to be poached in south-west France where an illegal tradition is supposed to kill up to 50 000 birds annually (Claessens 1992) while the Scandinavian breeding populations are rapidly disappearing (Vepsäläinen et al. 2005). Beyond the Aquatic Warbler, the method can be applied to any large datasets of ringing and recovery of migrant bird, and will be particularly appropriate for small species such as passerines with restricted flight range when in Europe (Arizaga et al. 2011).

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REFERENCES


STRESZCZENIE

[Szacunkowa liczebność wodniczek zatrzymujących się we Francji podczas jesiennej wędrówki] Wydaje się, że znacząca większość wodniczek lecąc na zimowiska do Afryki wędruje wzdłuż wybrzeży zachodniej Europy. Autorzy na podstawie analizy danych uzyskanych z obrączkowania stali się oszacować liczebność populacji tego gatunku korzystającej z miejsc przystankowych znajdujących się we Francji. Wielkość całej światowej populacji wodniczki w okresie połogowym, została oszacowana na podstawie danych literaturoowych.

W 2009 obrączkarze we Francji przeprowadzili akcję łapania ptaków dedykowaną wodniczce, mającą na celu zwiększenie częstotliwości chwytania tego gatunku. Wędrujące ptaki wabiło w siedliskach odpowiednich na miejsca przystankowe nagranymi glosami. W efekcie pracy 44 punktów obrączkarskich łącznie schwytano 874 różne osoby. W 2010 prace te powtórzono i zaobrączkowano 646 osobników.

Na podstawie danych uzyskanych przez obrączkowanie i ponowne schwytanie części z tych ptaków, zaprezentowana została prosta metoda oszacowania liczby osobników (wszystkich jak i wyłącznie młodych wyklutych w danym sezonie), które zatrzymują się na terenie Francji podczas jesiennej wędrówki. Teren Francji podzielono na dwie części — północną i południową. Dla porównania wielkość uzyskanych szacunków zastosowano trzy granice podziału kraju (Fig. 1). Do szacowania liczby osobników zatrzymujących się we Francji użyto całkowitą liczbę schwytanych ptaków oraz liczbę ptaków zaobrączkowanych na północy kraju i złapanych ponownie południu.

Na podstawie danych literaturoowych stwierdzono, że w zależności od sezonowej zmienności w sukcesie lęgowym i przeżywalności, populacja Wodniczki w okresie jesiennej wędrówki liczby pomiędzy 23 a 69 tys. osobników, w tym 5–44 tys. osobników młodych, wykluczych w danym sezonie. Na podstawie szacunków wynikających z liczby zaobrączkowanych wodniczek we Francji, stwierdzono, że na miejscach przystankowych w tym kraju zatrzymuje się między 24 a 30 tys. osobników tego gatunku, w większości w pierwszym roku życia (Tab. 1). Te wyliczenia wskazują,
że prawdopodobnie wszystkie młode, jednoroczne wodniczki lecą zachodnim szlakiem przelotu przez wybrzeża Francji, zatrzymując się na istniejących tu dogodnych miejscach przystankowych. Natomiast ptaki dorosłe albo wykorzystują przynajmniej częściowo inną trasę przelotu, lub też zatrzymują się we Francji krócej lub w mniejszej liczbie miejsc. Wyliczone szacunki liczebności wędrujących wodniczek podkreślają znaczenie utrzymania odpowiednich miejsc przystankowych dla tego gatunku wzdłuż całego wybrzeża Francji.