Ringing & Migration

ISSN: 0307-8698 (Print) 2159-8355 (Online) Journal homepage: https://www.tandfonline.com/loi/tram20

# Differential post-breeding movements of Cetti's Warblers *Cettia cetti* in two reedbeds in south-west France

Jean-Marc Fourcade & Philippe Fontanilles

**To cite this article:** Jean-Marc Fourcade & Philippe Fontanilles (2019): Differential post-breeding movements of Cetti's Warblers *Cettia cetti* in two reedbeds in south-west France, Ringing & Migration, DOI: 10.1080/03078698.2018.1629115

**To link to this article:** https://doi.org/10.1080/03078698.2018.1629115

RINGING & MIGRATION
https://doi.org/10.1080/03078698.2018.1629115

# Differential post-breeding movements of Cetti's Warblers *Cettia cetti* in two reedbeds in south-west France

Jean-Marc Fourcade and Philippe Fontanilles

Observatoire d'Intérêt Scientifique Ornithologique, 65 route de Saint-Pierre-d'Irube, F-64990 Villefranque, France

**ABSTRACT**
Differential post-breeding movements between sex or age groups lead to spatial segregation and can result in the exploitation of different habitats by individuals from the same population. Our aim is to assess whether the use of reedbeds by non-breeding Cetti's Warblers *Cettia cetti* involves many transients arriving and departing throughout autumn, or a brief dispersal into this habitat after which individuals stay for a prolonged period. We sampled two reedbeds in south-west France: one dry, or flooded by rain, composed of small mixed reeds, and another with tall reeds and influenced by tidal flooding. We analysed daily capture–recapture data in autumn for two years in each reedbed. Capture–recapture analysis did not detect transients and showed a weak transit dynamic, with some immigration, mainly in the first half of September, and negligible emigration. Thus, reedbeds are used by dispersing birds, mostly the same individuals, with at both sites a strong majority of young females. We interpret this segregation as a product of intraspecific competition. We also noted a higher proportion of adult birds in the dry reedbed (27.6%, with equal sex ratio; more similar to habitats used throughout the year) than in the flooded one (11.7%, with 83.3% being females; unsuitable for breeding). These findings have important implications for the significance of reedbed habitat to this species. Its sustained use by young females makes Cetti's Warbler vulnerable to the loss of reedbed, or its degradation due to growth of shrubby vegetation or the lack of suitable management.

**ARTICLE HISTORY**
Received 2 July 2018
Accepted 14 November 2018

In resident species, post-breeding movements or dispersals are a one-way movement with no primary direction (Newton 2008). Most natal dispersal of juveniles, between hatching place and first breeding site, and breeding or winter dispersal of some adults is at a local scale, although some juveniles may disperse over long distances (Greenwood & Harvey 1982, Newton 2008). This behaviour leads to genetic exchange and the avoidance of inbreeding, and plays a key role in metapopulation and source–sink dynamics (Paradis *et al* 1998). It may facilitate competition avoidance, density regulation and the colonisation of new breeding grounds (Newton 2008). These dispersal movements are dependent upon sex and age: usually, males move shorter distances than females and adults shorter distances than juveniles (Greenwood 1980, Paradis *et al* 1998). The general pattern of female-biased dispersal is because of the male's site fidelity through a resource-defending mating system. They benefit from familiarity with an area by increasing their reproductive performance, for example through knowledge of safe breeding sites, foraging efficiency, predator avoidance or prior residency (Greenwood 1980, Pusey 1987).

Cetti's Warbler *Cettia cetti* is an insectivorous passerine that breeds in western and southern Europe, where it is largely sedentary (Kennerley & Pearson 2010). Males are larger than females, and exhibit a territorial polygyny in which males hold large breeding territories and mate with up to three females (Bibby 1982, Cramp 1992). Western populations are mainly restricted to wetlands but avoid homogeneous and flooded reedbeds during the breeding period: thick, low woody vegetation is generally required for permanent residency (Cramp 1992, Kennerley & Pearson 2010). Nevertheless, Araújo et al (2016) showed Cetti's Warbler exploited reedbeds during the non-breeding period for appropriate shelter and food resources. Post-breeding dispersal takes place mainly during September and early October when an influx of predominantly young females occurs into the reedbeds (Bibby & Thomas 1984, Kennerley & Pearson 2010). In Iberia and France some individuals overwinter in reedbeds from November to February and then leave during March (Cantos 1992, Neto 2003, Bargain & Henry 2005, Araújo *et al* 2016).

The composition of the post-breeding influx into reedbeds has been studied by Bibby & Thomas (1984)

**CONTACT** Jean-Marc Fourcade ✉ jmarcfourcade@gmail.com

who suggested that young females are displaced from the most suitable habitats, occupied during the breeding period, and that males move to a lesser extent because they hold territories from autumn onward. Earlier studies focused on young birds (Bibby & Thomas 1984) or on the overall sex ratio (Villarán 2000, Neto 2003, Balança & Schaub 2005, Bargain & Henry 2005). More recently, Araújo et al (2016) showed that, in the reedbeds they studied, increasing numbers of adult birds were captured during the autumn. To clarify this mixed picture, additional analyses by age and sex class are required to identify the proportion of adults of each sex that enter the reedbeds in autumn.

Different movement strategies lead to differential usage of reedbeds. Birds can be very mobile over the period, moving between potentially diverse sites (reedbed, wooded swamp, riparian forest) and staying briefly. In such a scenario, high rates of immigration into and emigration from the reedbeds would be expected. In contrast, low rates of immigration and emigration would indicate greater population stability, with sustained exploitation of reedbed resources by the same individuals. Over a two-year study on the Mediterranean coast, Balança & Schaub (2005) found low probabilities of immigration and emigration in one of the years but in the other year a significant proportion of transients (i.e. individuals that left the study site between the first capture and the next sampling occasion). However, the average time interval between sampling occasions in their study was seven days. A new description of post-breeding movements with daily sampling would allow a more accurate estimation, especially of possible transients.

Cetti's Warblers' use of reedbeds, which are a globally threatened habitat (Tucker & Heath 1994), with post-breeding movements that are dependent upon sex and age, raises conservation issues. Differential movements lead to a spatial segregation throughout the non-breeding period. One consequence of this is that factors determining survival can vary among individuals of the same population or between groups of individuals by age, sex and size (Newton 1998, Cristol *et al* 1999, Marra & Holmes 2001). Differences in habitat quality, acting for example through food resources, intra- and interspecific competition, predation risk or parasitism, can lead to divergent mortality rates and may also influence body condition on a long-term scale. Knowledge of differential movements of a species is required, therefore, to understand their modalities and deduce the implications for conservation, particularly those related to the use of different habitats by individuals of the same population (Cristol *et al* 1999). Cetti's Warbler is not currently threatened in Europe and has the 'Least Concern' global conservation category (BirdLife International 2018). In France, however, its status was reassessed recently as 'Near Threatened' (IUCN France *et al* 2016).

Our study analysed daily capture–recapture data from two reedbeds. Our primary aim was to assess whether Cetti's Warblers have a long period of high mobility and transitory use of reedbeds during dispersal, or a short displacement and sustained use of this habitat. In addition, we evaluate the importance of reedbed for the age and sex classes with a focus on adults during autumn.

## Material and methods

### *Study site*

The study site is a wetland of 300 ha, with mixed habitats, near the Adour estuary in south-west France (43°27'N 1°29'W). It belongs to the Natura 2000 network and is classified as Sensitive Natural Area. Two reedbeds were sampled at Villefranque and Bayonne, 1.5 km apart, as described by Fontanilles *et al* (2017). The site at Villefranque is a degraded reedbed of 7.5 ha, composed of small reeds, flooded by rainwater in winter and spring but dry in summer and autumn (facilitating the encroachment of *Carex* species and bindweeds *Convolvulus*), and bordered mainly by thickets of willow (*Salix*) which encroach into the reedbed. The Bayonne site is a 7.5-ha reedbed where tall reeds are flooded daily by the tide, with some scattered small patches of willow on drier parts, bordered mainly by willow thickets. The Cetti's Warbler breeds at the edges of the study sites and feeds in the reedbeds, a situation commonly observed in this species (Kennerley & Pearson 2010, Araújo *et al* 2016).

### *Data collection*

Data was obtained by daily sampling, over two years at each site: at Villefranque from 1 August to 2 October in 2010 and from 18 July to 31 October in 2011; at Bayonne from 30 July to 1 October in 2012 and 4 August to 30 September in 2015. Cetti's Warbler was captured during a wider study on migratory birds. Sound lures (Aquatic Warbler *Acrocephalus paludicola* for some nets and a mix of *Sylvia* warblers for others) were used identically each year, except in 2015 when the song of Bluethroat *Luscinia svecica* was added. The lures were turned on as the nets were opened. These lures have potential effects on capture rates and on age and sex ratios for the target species (e.g. Brotons 2000, Lecoq & Catry 2003, Arizaga *et al* 2015). The potential effects on other species are not widely acknowledged but de la Hera *et al* (2017) showed an increase in capture rates and highlighted the need for a standardised protocol to work with constant bias.

Cetti's Warblers were captured with mist nets opened for five or six hours after dawn: 240 m in 2010 and 252 m in 2011 in Villefranque, and 180 m in 2012 and 216 m in 2015 in Bayonne. Birds were ringed, measured (maximum wing length) and weighed. Sex was determined *a posteriori* from the wing length (female if $\leq 58$ mm and male if $\geq 62$ mm; Demongin 2013) and according to our own data on body mass of local individuals (values valid only from sunrise to noon): young birds, female if body mass $\leq 11.2$ g and male if $\geq 12.6$ g; adults, female if $\leq 12.7$ g and male if $\geq 12.8$ g (Fourcade & Fontanilles 2014). Birds were aged following Demongin (2013): young (EURING code 3) or adult (EURING code 4). We distinguished four groups in the population: young and adult males, young and adult females. Only the first capture was considered. The frequencies were compared with chi-square and Fisher's Exact tests and departures from an even age or sex ratio were tested with a binomial test, performed in the R environment (R Core Team 2016).

Post-breeding movements of western populations begin in late August or early September (Cramp 1992, Kennerley & Pearson 2010) and our data were consistent with this pattern (see Results). We therefore split our study into two periods, following Araújo *et al* (2016): late summer (1–28 August) and autumn (29 August to 30 September). The date of division corresponds to standard pentads (Berthold 1973). In line with annual variations in breeding phenology, some individuals can move early, in late summer, and the population then consists of 'resident' birds (breeding adults or young hatched at the edges of the sites) and moving birds (our target population), which cannot be distinguished at the time of marking. By contrast, we considered that all unmarked individuals caught in autumn were undertaking post-breeding movements, because the daily sampling in late summer enabled us to mark almost all individuals already on site.

### *Immigration and emigration*

The study focused on the autumn period (with 33 encounter occasions) because the low numbers caught in late summer did not allow for global analysis. Any individual marked in late summer was excluded. Sex was not considered, due to a small sample size for males. Because we investigated both immigration and emigration, we used Pradel models for open populations, which give separate estimates of local survival ($\phi$), seniority ($\gamma$) and recapture probability (p) (Pradel 1996, Morris *et al* 2005). But if transients occur, models dealing with seniority cannot be applied because information about capture probability of the transients is missing (Nichols *et al* 2000). We checked the fit of data to model assumptions with U-CARE software for the most complete model $\phi_{year*t}$ $p_{year*t}$ $\gamma_{year*t}$, including the specific subtest 3.SR to detect transience (Choquet *et al* 2005). As we did not detect transients (see Results), these models were appropriate to use. They were run in MARK 8.0 software (White & Burnham 1999). We used these models in the same way as for stopover duration studies in long-distance migrants: because the daily emigration probabilities are an order of magnitude higher than the daily mortality probabilities (i.e. the actual daily survival is assumed to be unity ; Schaub *et al* 2004, Schaub 2006, Chernetsov 2012), the emigration probability ($\varepsilon$) is calculated by $\varepsilon = 1 - \phi$; and because there is no birth, the immigration probability ($\iota$) is calculated by $\iota = 1 - \gamma$. We tested year as effect and parameters $\varepsilon$ and $\iota$ could be time dependent (t), a linear function of time (T) or constant across time (.). The recapture probability could be time dependent ($p_t$), constant (p.) or, because of the variation in the length of mist nets between years, depending on the capture effort ($p_{effort}$) expressed as mist-net length x hours of opening. The corrected Akaike Information Criterion ($AIC_c$) was used to rank the fit of models. The model with the lowest $AIC_c$ was considered the best. An $AIC_c$ difference ($\Delta AIC_c$) > 2 indicated a considerably less plausible model (Burnham & Anderson 1998). The parameter estimability near the boundaries (0, 1) was validated by data cloning, according to the procedure described by Cooch & White (2016).

## Results

Few birds were caught during late summer in both sites, then an increase was noticeable throughout autumn (Figure 1). Because the capture chronology was similar between years at both sites (Wilcoxon test: Villefranque, W = 867.5, $P = 0.106$; Bayonne, W = 3780, $P = 0.091$), the two years were pooled. No capture peak was noticeable in autumn, with maxima of 4.3 individuals per100 m of mist net per hour at Villefranque and 9.5 at Bayonne.

### *Immigration and emigration*

The data fitted the model assumptions according to the overall test ($\chi^2_{127} = 31.63$, $P = 1$) and to the specific tests for trap dependence (3.CT test $P_{two\text{-}tailed} = 0.145$)

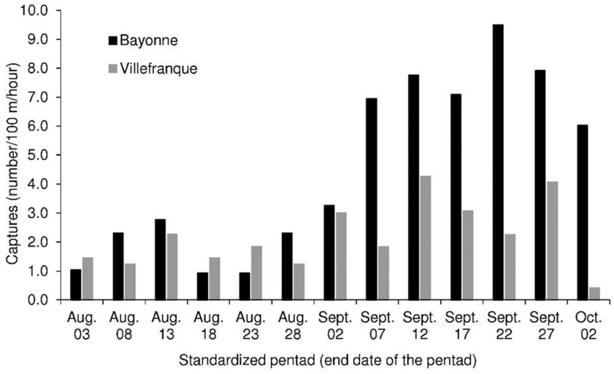

**Figure 1.** Standardised number of birds captured (number per 100 m of net per hour) by pentad in Villefranque (2010, 2011) and Bayonne (2012, 2015).

and transience (3.SR test $P_{\text{one-tailed}} = 0.231$). The latter result meant that the population did not include a significant proportion of transient individuals. A single model was selected (Table 1). The year had no significant effect on the result as indicated by the best model. Recapture probability was very low and dependent on the capture effort (mean 0.025 ± 0.008 SD). Emigration probability was very low and constant over time ($\varepsilon = 0.004$, 95% confidence interval 0.000–0.026). Immigration probability showed a seasonal decreasing trend, from 0.136 (0.058–0.255) in late August to low values in late September ($\iota = 0.007$, 0.001–0.027) (Figure 2).

## *Age and sex classes*

At both sites, in late summer and autumn, the frequency of age and sex classes was similar between years (Fisher's Exact Tests: all NS; Table 2). For clarity and to increase the sample size, the two years were pooled for each site for subsequent analyses.

At Villefranque, the sex ratio was balanced during late summer both for young birds (n = 38, Binomial Test: $P = 0.143$) and adults (n = 7, $P = 0.453$). In autumn, sex ratio remained balanced for adults (n = 21, $P = 0.189$) but not for young birds (85.5% females, n = 55, $P < 0.0001$). The age ratio was skewed against adults, which constituted just 27.6% of individuals entering the reedbed (n = 76, $P = 0.0001$).

**Table 1.** Pradel model selection to estimate the probabilities of emigration (ε), recapture (p) and immigration (ι): K, number of parameters; AIC$_c$, corrected Akaike Information Criterion; ΔAIC$_c$, difference in AIC values between each model and the best model; (.), constant over time; (effort), trapping effort; (T), linear trend of time. Only the top-ranked models are shown, with the selected model first.

| Model | K | AIC$_c$ | ΔAIC$_c$ | AIC$_c$ weights | Model likelihood |
|---|---|---|---|---|---|
| ε(.) p(effort) ι(T) | 5 | 3077.561 | 0.000 | 0.956 | 1.000 |
| ε(.) p(effort) ι(.) | 4 | 3085.243 | 7.682 | 0.021 | 0.022 |
| ε(T) p(effort) ι(.) | 5 | 3086.163 | 8.603 | 0.013 | 0.014 |
| ε(T) p(.) ι(T) | 5 | 3088.083 | 10.523 | 0.005 | 0.005 |
| ε(year) p(effort) ι(.) | 7 | 3088.511 | 10.950 | 0.004 | 0.004 |

At Bayonne, the sex ratio was balanced during late summer, both for young birds (n = 37, $P = 1$) and adults (n = 6, $P = 0.688$) and then unbalanced for both age classes in autumn (young birds: 87.3% females, n = 181, $P < 0.0001$; adults: 83.3% females, n = 24, $P = 0.002$). Adult males accounted for 2% of the total catches. The age ratio was shifted against adults, which constituted just 11.7% of individuals entering the reedbed (n = 205, $P < 0.0001$).

The sites differed in autumn (contingency test: $\chi^2_3 = 12.69$, $P = 0.005$): more adults of both sexes were caught at Villefranque whereas adult males were nearly absent at Bayonne.

## Discussion

Immigration and emigration probabilities indicate a weak transit dynamic, with some immigration mainly in the first half of September and negligible emigration. These results indicate a low turnover of individuals through the study period and even higher stability of the population in the second half of September. We did not detect transients, which are individuals only passing through the study site without actually making use of it (called 'flyers' by Chernetsov 2012). Birds do not perform local nomadism with multiple shifts from site to site but rapidly change habitat, stop over and use the resources (these are called 'feeders' by Chernetsov 2012). Therefore, reedbeds free of established territories are a target habitat in autumn for Cetti's Warblers. Their loss, particularly through the

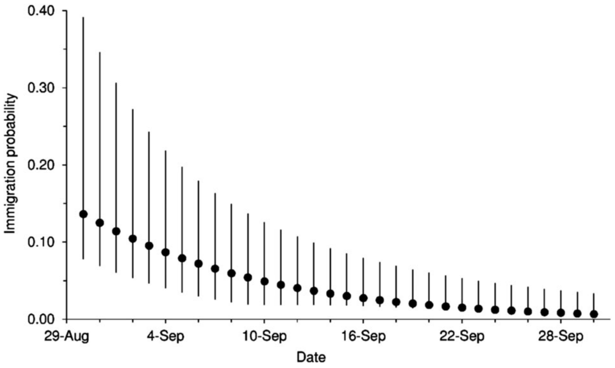

**Figure 2.** Immigration probabilities through the autumn period estimated with the best model, ε(.) p(effort) ι(T), which allows a linear time trend for this parameter. Error bars represent 95% confidence intervals.

**Table 2.** Detailed data of population structure per site and per year (late summer, 1–28 August; autumn, 29 August to 30 September). The Fisher's Exact Test tested the frequencies of the four age and sex classes between years.

| | | | | Adult | | Juvenile | | |
|---|---|---|---|---|---|---|---|---|
| Site | Year | Season | n | male | female | male | female | Fisher's Exact Test |
| Villefranque | 2010 | late summer | 26 | 1 | 3 | 8 | 14 | |
| | 2011 | late summer | 19 | 1 | 2 | 6 | 10 | $P = 1$ |
| Villefranque | 2010 | autumn | 35 | 5 | 9 | 4 | 17 | |
| | 2011 | autumn | 41 | 2 | 5 | 4 | 30 | $P = 0.129$ |
| Bayonne | 2012 | late summer | 14 | 2 | 1 | 7 | 4 | |
| | 2015 | late summer | 29 | 0 | 3 | 11 | 15 | $P = 0.124$ |
| Bayonne | 2012 | autumn | 98 | 1 | 7 | 10 | 80 | |
| | 2015 | autumn | 107 | 3 | 13 | 13 | 78 | $P = 0.441$ |

growth of shrubby vegetation suitable for breeding and permanent occupation by Cetti's Warblers, reduces the space for migrants searching in autumn for vacant areas. Extending the search for new sites would result in longer and more hazardous movements, with increased energy costs and a greater risk of predation. The effects would be harmful as it was recently shown that females, which form the majority of migrants, may suffer higher mortality in autumn and winter than in spring and summer (Monticelli *et al* 2014).

In late summer, few birds used the two reedbeds. Young birds and adults both showed equal sex ratios but our sample of adults was too low to obtain a robust estimate.

In autumn, at both Villefranque and Bayonne, movements involve mostly juveniles and mostly young females. This corresponds with previous studies on western populations (e.g. Bibby & Thomas 1984, Cramp 1992, Araújo *et al* 2016). The result is a local segregation of the population, mainly explained by intraspecific competition (Cristol *et al* 1999). Dominance relationships act on habitat or micro-habitat scales (Marra 2000). Young birds, females or small individuals behave as subordinates and occupy suboptimal habitats (Catry *et al* 2004, Tellería & Pérez-Tris 2004). This behaviour can be a trade-off. They get advantage by departing if the benefits of reduced competition are higher than the cost of using a less suitable habitat (Newton 1998), although females may also have innate differences from males in habitat selection (Morton *et al* 1987, Morton 1990). Reedbed could be better suited than other wetland types to vulnerable, inexperienced young birds. Its carrying capacity for passerines during autumn migration can be high, because of its large quantity of food resources (Chernetsov 1998, Chernetsov & Manukyan 1999, Kerbiriou *et al* 2010) that can be exploited by Cetti's Warblers (Bibby & Green 1983). Araújo *et al* (2016) observed higher food availability in a reedbed than in a nearby riparian habitat used by Cetti's Warblers. A lower risk of predation could be another hypothesis, especially near the ground where they forage for food.

We found an equal sex ratio for adults at Villefranque. In autumn, this reedbed has some similarities to habitats used throughout the year, especially the mixed reeds and unflooded soil available for their foraging on or near the ground (Bibby & Green 1983). Conversely, the adult sex ratio was strongly biased towards females at Bayonne: this reedbed appears unfavourable for a permanent settlement, because of its homogeneous plots of tall reeds and daily tidal flooding. Additionally, the sex ratio is consistently more skewed towards females in homogeneous reedbeds than in mixed ones (Bibby & Thomas 1984, Neto 2003, Balança & Schaub 2005, Bargain & Henry 2005). Adult males are almost absent in the tall, daily flooded reeds of Bayonne. The males' territoriality is strong and persists throughout the year, as shown by their winter songs. Wintering in an unsuitable habitat would not benefit their future breeding. In south-west France, similar poor numbers of adult females and young males were found in flooded reedbed in autumn. This might suggest that for these two groups, experience from age and dominance from size act similarly. In some species, age and experience can have a greater influence on spatial segregation than size dimorphism and dominance: Smith *et al* (1993) showed that the frequency of adult female Snow Buntings *Plectrophenax nivalis*, another passerine with strong sexual size dimorphism, increased towards better wintering grounds, unlike young males.

To conclude, the post-breeding movements of Cetti's Warbler represent an extreme case of spatial segregation at a local scale, with a strong attraction of young females to reedbeds. Adults had an equal sex ratio in the dry reedbed but male adults were very rare in the flooded reedbed and avoid settling in this habitat, thus strengthening the spatial segregation. The autumn influx into reedbeds was followed by a strong stability of the population during the study duration. The conservation of reedbeds is part of the protection of

Cetti's Warbler, as its seasonal target habitat. But this habitat is among the most threatened in France and in Europe (Tucker & Heath 1994, Rocamora & Yeatman-Berthelot 1999). Their degradation, particularly through the growth of shrubby vegetation or abandonment of management, would make them relevant for breeding and permanent occupation, but expel many young immigrants in search of vacant areas where intraspecific competition is reduced. Due to spatial segregation, a loss of this habitat affects particularly the young individuals which are the majority of settlers in the reedbeds. These young birds are identified as pioneers in geographical conquest or recolonisation following population collapse (Robinson *et al* 2007, Kennerley & Pearson 2010). Suitable management is required to preserve reedbed habitats and this can also benefit other bird species throughout the year.

## Acknowledgements

We are grateful to the people who assisted us during the field work: Michel Borie, Bernard Chanchus, Xavier Chauby (RNCFS d'Arjuzanx), Christophe De Franceschi, Laurent Demongin, Laurent Dufresne, Jean Michel Lapios, Francis Lartigau, Roger Short, Pèire Thouy, Patrice Urbina-Tobias, the late Bernard Van Acker, Melchior Viallet and all volunteers. This study was funded by Conseil Départemental des Pyrénées-Atlantiques, Syndicat Mixte de la Nive Maritime, and the Bayonne and Villefranque municipalities. The National Museum of Natural History in Paris gave us permission to carry out ringing activities. We particularly thank: François Esnault (Conseil Départemental des Pyrénées-Atlantiques), Pierre-Yves Henry (CRBPO/MNHN), Maxime Diribarne (Syndicat Mixte de la Nive Maritime), Axelle Fronzes, Lionel Sevilla (Bayonne), Charles Hopper, Marijo Carita, and two anonymous reviewers for useful comments on an earlier version of the manuscript.

## References

**Araújo, P.M., Lopes, P.B., da Silva, L.P. & Ramos, J.A.** (2016) The importance of reedbeds and riparian areas for Cetti's Warbler *Cettia cetti* throughout its annual cycle. *Wetlands* **36**, 875–887.

**Arizaga, J., Musseau, R., Laso, M., Esparza, X., Unamuno, E., Azkona, A. & Fontanilles, P.** (2015) Biases associated with the use of a playback in stopover ecology studies of Bluethroats *Luscinia svecica*. *Bird Study* **62**, 280–284.

**Balança, G. & Schaub, M.** (2005) Post-breeding migration ecology of Reed *Acrocephalus scirpaceus*, Moustached *A. melanopogon* and Cetti's Warblers *Cettia cetti* at a Mediterranean stopover site. *Ardea* **93**, 245–257.

**Bargain, B. & Henry, J.** (2005) Les oiseaux de la Baie d'Audierne. Analyse des données de la station de baguage de 1998 à 2003. *Penn Ar Bed* **193/194**, 1–72.

**Berthold, P.** (1973) Proposals for the standardization of the presentation of data of annual events, especially of migration data. *Auspicium* **5** (suppl.), 49–59.

**Bibby, C.J.** (1982) Polygyny and the breeding ecology of the Cetti's Warbler *Cettia cetti*. *Ibis* **124**, 288–301.

**Bibby, C.J. & Green, R.E.** (1983) Food and fattening of migrating warblers in some French marshlands. *Ringing & Migration* **4**, 175–184.

**Bibby, C.J. & Thomas, D.K.** (1984) Sexual dimorphism in size, moult and movements of Cetti's Warbler *Cettia cetti*. *Bird Study* **31**, 28–34.

**BirdLife International** (2018) Species factsheet: *Cettia cetti*. The IUCN Red List of Threatened Species. Downloaded from www.birdlife.org on 18 Feb 2018.

**Brotons, L.** (2000) Attracting and capturing Coal Tits *Parus ater*: biases associated with the use of tape lures. *Ringing & Migration* **20**, 129–133.

**Burnham, K.P. & Anderson, D.R.** (1998) *Model selection and inference: a practical information theoretic approach*. Springer-Verlag, New York.

**Cantos, F.J.** (1992) *Migración e invernada de la familia Sylvidae (Orden Passeriformes, Clase Aves) en la península Ibérica*. PhD thesis. Universidad Complutense de Madrid, Madrid.

**Catry, P., Campos, A., Almada, V. & Cresswell, W.** (2004) Winter segregation of migrant European Robins *Erithacus rubecula* in relation to sex, age and size. *Journal of Avian Biology* **35**, 204–209.

**Chernetsov, N.** (1998) Habitat distribution during the post-breeding and post-fledging period in the Reed Warbler *Acrocephalus scirpaceus* and Sedge Warbler *A. schoenobaenus* depends on food abundance. *Ornis Svecica* **8**, 77–82.

**Chernetsov, N.** (2012) *Passerine Migration: stopovers and flight*. Springer-Verlag, Berlin.

**Chernetsov, N. & Manukyan, A.** (1999) Feeding strategy of Reed Warblers *Acrocephalus scirpaceus* on migration. *Avian Ecology and Behaviour* **3**, 59–68.

**Choquet, R., Reboulet, A.M., Lebreton, J.-D., Gimenez, O. & Pradel, R.** (2005) *U-CARE 2.2 User's Manual*. CEFE, Montpellier, France.

**Cooch, E.G. & White, G.C.** (2016) *Program Mark – a gentle introduction*. 17th edition. www.phiorg/software/mark/docs/book

**Cramp, S.** (1992) *The Birds of the Western Palearctic*. Volume VI: Warblers. Oxford University Press, Oxford.

**Cristol, D.A., Baker, M.B. & Carbone, C.** (1999) Differential migration revisited: latitudinal segregation by age and sex class. *Current Ornithology* **15**, 33–88.

**De la Hera, I., Fontanilles, P., Delalande, L., Glad, A. & Sarraude, T.** (2017) Attraction of other species by Bluethroat *Luscinia svecica* song playback during autumn migration: an experimental test using bird-ringing data. *Ardeola* **64**, 91–99.

**Demongin, L.** (2013) *Guide d'identification des oiseaux en main*. Mortsel, Belgium.

**Fontanilles, P., Brongo, M., De La Hera, I., Fourcade, J.M., Keller, A., Lapios, J.M. & Sourdrille, K.** (2017) Do flooded reedbeds stopover more migratory passerines than dry reedbeds? Habitat structure and avifauna community are compared. *Alauda* **85**, 161–178. [In French.]

**Fourcade, J.M. & Fontanilles, P.** (2014) Détermination du sexe chez la Bouscarle de Cetti *Cettia cetti* en automne dans le sud-ouest de la France. *Le Casseur d'Os* **14**, 110–118.

**Greenwood, P.J.** (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28**, 1140–1162.

**Greenwood, P.J. & Harvey, P.H.** (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* **13**, 1–21.

**IUCN France, MNHN, LPO, SEOF & ONCFS** (2016) *La Liste rouge des espèces menacées en France – Chapitre Oiseaux de France métropolitaine*. Paris, France.

**Kennerley, P. & Pearson, D.** (2010) *Reed and Bush Warblers.* Christopher Helm, London.

**Kerbiriou, C., Bargain, B. & Le Viol, I.** (2010) Diet and fuelling of the globally threatened Aquatic Warbler at autumn stopover as compared with two congeners. *Animal Conservation* **14**, 261–270.

**Lecoq, M. & Catry, P.** (2003) Diurnal tape-luring of wintering Chiffchaffs results in samples with biased sex ratios. *Journal of Field Ornithology* **74**, 230–232.

**Marra, P.P.** (2000) The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the non-breeding season. *Behavioral Ecology* **11**, 299–308.

**Marra, P.P. & Holmes, R.T.** (2001) Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *Auk* **118**, 92–104.

**Monticelli, D., Pedro, M., Araújo, P.M., Hines, J.E., Tenreiro, P.Q., Silva, L.P. & Ramos, J.A.** (2014) Assessing the role of body mass and sex on apparent adult survival in polygynous passerines: a case study of Cetti's Warblers in central Portugal. *Journal of Avian Biology* **45**, 75–84.

**Morris, S.R., Liebner, D.A., Larracuente, A.M., Escamilla, E.M. & Sheets, H.D.** (2005) Multiple-day constancy as an alternative to pooling for estimating mark–recapture stopover length in Nearctic–Neotropical migrant land birds. *Auk* **122**, 319–328.

**Morton, E.S.** (1990) Habitat segregation by sex in the Hooded Warbler: experiments on proximate causation and discussion of its evolution. *American Naturalist* **135**, 319–333.

**Morton, E.S., Lynch, J., Young, K. & Mehlhop, P.** (1987) Do male Hooded Warblers exclude females from nonbreeding territories in tropical forest? *Auk* **104**, 133–135.

**Neto, J.M.** (2003) Annual dynamics of reedbed passerines in Ria de Aveiro, Portugal, assessed by standardized mist-netting. *Airo* **13**, 17–29.

**Newton, I.** (1998) *Population Limitation in Birds*. Academic Press, London.

**Newton, I.** (2008) *The Migration Ecology of Birds*. Academic Press, London.

**Nichols, J.D., Hines, J.E., Lebreton, J.-D. & Pradel, R.** (2000) Estimation of contributions to population growth: a reverse-time capture–recapture approach. *Ecology* **81**, 3362–3376.

**Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D.** (1998) Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology* **67**, 518–536.

**Pradel, R.** (1996) Utilization of capture–mark–recapture for the study of recruitment and population growth rate. *Biometrics* **52**, 703–709.

**Pusey, A.E.** (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution* **2**, 295–299.

**R Core Team** (2016) *R: a language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

**Robinson, R.A., Freeman, S.N., Balmer, D.E. & Grantham, M.J.** (2007) Cetti's Warbler *Cettia cetti*: analysis of an expanding population. *Bird Study* **54**, 230–235.

**Rocamora, G. & Yeatman-Berthelot, D.** (1999) *Oiseaux menacés et à surveiller en France. Listes rouges et recherche de priorités. Populations. Tendances. Menaces. Conservation*. SEOF/LPO, Paris.

**Schaub, M.** (2006) How to study departure decisions of migrants from stopover places using capture–recapture data. *Acta Zoologica Sinica* **52** (suppl), 602–605.

**Schaub, M., Liechti, F. & Jenni, L.** (2004) Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. *Animal Behaviour* **67**, 229–237.

**Smith, R.D., Marquiss, M., Rae, R. & Metcalfe, N.B.** (1993) Age and sex variation in choice of wintering site by Snow Buntings: the effect of altitude. *Ardea* **81**, 47–52.

**Tellería, J.L. & Pérez-Tris, J.** (2004) Consequences of the settlement of migrant European Robins *Erithacus rubecula* in wintering habitats occupied by conspecific residents. *Ibis* **146**, 258–268.

**Tucker, G.M. & Heath, M.F.** (1994) *Birds in Europe: their conservation status*. BirdLife International, Cambridge, UK.

**Villarán, A.** (2000) Biometría, fenología y razón de sexos del Ruiseñor Bastardo *Cettia cetti* en carrizales del Valle del Tajo (España central). *Butlletí del Grup Català d'Anellament* **17**, 1–9.

**White, G.C. & Burnham, K.P.** (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, 120–139.