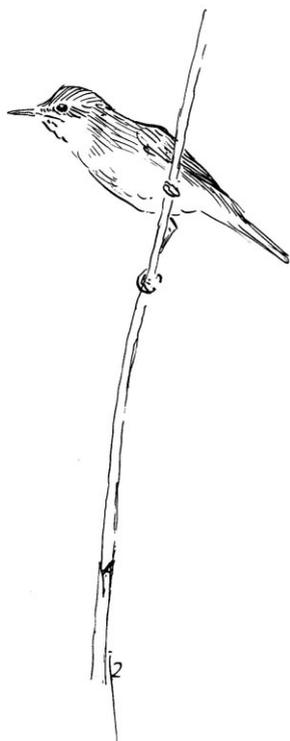


# Post-breeding migration ecology of Reed *Acrocephalus scirpaceus*, Moustached *A. melanopogon* and Cetti's Warblers *Cettia cetti* at a Mediterranean stopover site

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We analysed and compared body mass and capture-recapture data of a long-distance migrant, the Reed Warbler *Acrocephalus scirpaceus*, and of two partial and short-distance migrants, the Moustached Warbler *A. melanopogon* and the Cetti's Warbler *Cettia cetti*. Data were collected during two consecutive autumn seasons at a Mediterranean stopover site in southern France. Mean stopover duration of Reed Warbler was 8.5 days. It increased from 6.1 days at the end of July to 11.1 days at the end of October. The fuel deposition rate of Reed Warblers was 0.29 g day<sup>-1</sup> at the peak of migration (end of September) and 0.40 g day<sup>-1</sup> in late October. The gain in body mass during stopover was 0.37 g in late July and 4.48 g in late October. Although the stopover duration was longer at the end of the season, the longer potential flight range may have enabled them to achieve a higher migration speed. In contrast to the Reed Warbler, immigration and emigration probabilities of Moustached and Cetti's Warblers to and from the stopover site were low, resulting in long stopover duration during which they did not significantly change body mass, irrespective of moult, sex or age. We discuss possible migration strategies of these three warbler species under consideration of ring recoveries.

Key words: *Acrocephalus*, *scirpaceus*, *melanopogon*, *Cettia*, migration, stopover ecology

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## INTRODUCTION

Passerine migratory journeys between breeding and wintering sites consist of short phases of flight during which energy is used and of longer phases of stopovers during which energy is accumulated (Berthold 1996). The migration strategies are

modulated by various environmental and endogenous factors (Jenni & Schaub 2003), among the most important ones are the spatio-temporal variation of food resources. The energetically demanding moult also needs to be timed in such a way that interference with fattening is minimised (Jenni & Winkler 1994). Therefore the migration

strategies may differ between species (Bibby & Green 1981, Bairlein 1991, Ellegren 1993, Fransson, 1995, Jones 1995, Lindström *et al.* 1996, Schaub & Jenni 2000a), or populations (Dierschke & Delingat 2001).

Compared to the stopover ecology of long-distance migrants relatively little is known about the stopover ecology of short-distance migrants. It appears that the period during which short-distance migrants can be encountered at stopover sites is often much longer than that of long-distance migrants (Berthold *et al.* 1991) and that short-distance migrants do not increase body mass or only slightly (e.g. Kaiser 1992). The long observation period may be due to two reasons. Firstly, it may be the result of individual birds that stay a long time at the stopover site. Secondly, it is possible that it is due to a long migratory period of the species and not due to a long stopover period of individuals. Clearly these two patterns reflect completely different migration strategies, and its distinction is possible when data of marked birds are analysed. Comparative studies of closely related short- and long-distance migrants using the same habitat at the same time and exploiting similar food resources are promising to get better insights into how environmental variation modulates migration strategies.

The aim of this study is to compare the stopover ecology of the long-distance migrant Reed Warbler *Acrocephalus scirpaceus* with that of two partial and short-distance migrants Moustached Warbler *A. melanopogon* and Cetti's Warbler *Cettia cetti* during two autumn seasons at a Mediterranean stopover site. Reed Warblers breed almost all over in Europe, and they winter in Africa south of the Sahara desert (Cramp 1992). First-year Reed Warblers start post-breeding movements while still moulting and these movements turn into directed movements as moult is completed (Mukhin 2004). At an early stage stopover duration is long (Schaub & Jenni 2001), fuel deposition weak (Schaub & Jenni 2000a), and thus migration speed low. When moult is completed, stopover duration decreases (Schaub & Jenni 2001) and fuel deposition rate increases (Schaub & Jenni 2000b). The energy reserves remain low during most of the

autumn migration (Schaub & Jenni 2000a), thus the fat stores needed to cross the Sahara desert are accumulated at stopover sites situated shortly before crossing (Schaub & Jenni 2000a). Therefore stopover sites along the Mediterranean coast and in Northern Africa seem to be very important for a successful migration. Yet, stopover ecology at such sites is less studied (but see Schaub & Jenni 2000a, b, 2001, Bibby & Green 1981, Rguibi-Idrissi *et al.* 2003) than at Central European stopover sites (e.g. Bibby & Green 1983, Berthold *et al.* 1991, Literak *et al.* 1995, Kaiser 1996, Chernetsov 1998, Schaub & Jenni 2000a, b, 2001).

The breeding range of Moustached and Cetti's Warbler covers mainly the Mediterranean area, yet Moustached Warblers also breed in continental south-eastern Europe (Cramp 1992). Knowledge about migration of these two warblers species is limited. Individuals from Mediterranean populations of both species are considered to be residents or short-distance migrants (Cramp 1992, Dubois *et al.* 2000). Fuel deposition during the migration period was found to be low in Cetti's Warbler (Bibby & Green 1983), and for individuals from Mediterranean populations of Moustached Warbler it is unknown. However, increases of fuel stores have been observed mainly late in the season in Moustached Warblers from eastern Austria (Berthold *et al.* 1991). Moreover, these birds conduct a complete moult before they start to migrate (Leisler 1972).

We use recent advances in capture-recapture methodology to estimate immigration of birds to and emigration from the stopover site (Schaub *et al.* 2001). This allows us to evaluate whether there is a true passage of individuals or just the departure of resident birds and to estimate stopover duration (Schaub *et al.* 2001). We estimate body mass changes during stopover, test whether it differs among groups of birds (age, sex, moult status) and during the season, and describe the moulting pattern of the three species. Based on these results and under consideration of ring recoveries we derive proposals of the migration strategies for the three warbler species.

## MATERIAL AND METHODS

### Study site and data collection

The study area is the Réserve naturelle de l'Estagnol (43°31' N, 03°51' E) situated in southern France, near Montpellier, at a distance of 4 km from the coast of the Mediterranean Sea. The largest part of this wetland is covered by reed (*Phragmites australis*). We captured birds with mist nets placed in the reed bed (Fig. 1). In 2001, captures were conducted at two successive days every week (in June every 2 weeks) from 11 June to 31 October (37 capture days in total). During the main migration period (July to October) the total length of mist nets was 180 m. In 2002, sampling differed in three aspects: we caught birds at one day every week, the period considered was from 15 August to 14 December (17 capture days in total) and at most days the total lengths of mist nets was 120 m. The mist nets were placed at the same places in both years. They were open during six hours since dawn and checked every hour. The captured birds were individually ringed and the following data were recorded at each capture: date, time of weighing, age, body mass (taken with a Pesola spring balance to the nearest 0.5 g), and moult: a bird was considered moulting when at least 1 wing or 10 body feathers were growing. Cetti's Warblers were sexed and Moustached Warblers aged according to their wing length and tongue spots, respectively (Svensson 1992).

### Statistical analysis

Reed and Moustached Warbler breed at the study site, but only individuals that are on migration should be considered for the analyses. Based on phenology of reproduction (Cramp 1992) and on morphological traits (increase of mean wing length over the season in Reed Warbler suggesting increasing amount of northern individuals), we assumed that most individuals that were captured from 25 July were on migration, and thus included only those for the analyses. Cetti's Warblers breed in the bushes surrounding the reed bed and enter the reed bed after breeding only. Although they may start with these movements in July already,



**Figure 1.** Nets at the Réserve Naturelle de l'Estagnol, southern France (photo N. Gaidet).

we considered the period from 13 August onwards because sample size was too low before.

### Immigration, emigration and stopover duration

We constructed a capture history for each individual (a vector with elements 1 or 0 depending on whether or not the individual was captured at the corresponding capture occasion). For autumn 2001 we pooled all captures conducted at two successive days to one capture occasion. In 2002 we captured only at one day per capture occasion, so no pooling was necessary. The time intervals between capture occasions were variable (average 7 days, range 4–14 days) and were taken into account for estimating weekly immigration and emigration probabilities.

We analysed these individual capture histories with Cormack-Jolly-Seber models (Lebreton *et al.* 1992). This model allows the separation of the

recapture probability ( $p_i$ : probability to catch a marked bird at time  $i$  given that it is at the stopover site at time  $i$ ) from the local survival probability ( $\phi_i$ : probability that a marked bird is at the site at time  $i+1$ , given that it was at the site at time  $i$ ). Because the weekly emigration probabilities are an order of magnitude higher than the weekly mortality probabilities (Schaub in press), we assume that mortality during stopover is negligible, and thus the emigration probability ( $\epsilon$ ) can be calculated as  $\epsilon_i = 1 - \phi_i$ . To estimate the immigration probability ( $\iota$ ), we analysed the same data with a Cormack-Jolly-Seber model run backwards in time (Pradel 1996, Schaub *et al.* 2001). The estimates obtained are the recapture probability (denoted as  $r_i$ ) and the probability that a marked bird that is at the site at time  $i+1$  has been at the site already at time  $i$  (seniority probability denoted as  $\gamma_i$ ). Since no birds were born during the time periods considered, the immigration probability is simply calculated as  $\iota_i = 1 - \gamma_i$ . From these two probabilities stopover duration can be calculated (Schaub *et al.* 2001).

We tested whether the model assumptions of no heterogeneity among individuals were met by a goodness-of-fit test of a general model (see below) with program U-CARE (Choquet *et al.* 2001). Two kinds of heterogeneity may be expected in this study: the occurrence of a significant proportion of transients (transients are individuals that have left the study site before the next capture occasion following initial capture; Pradel *et al.* 1997) and immediate trap-response behaviour (catchability change when the individual was captured at the previous occasion compared to when it was not captured at the previous occasion; Pradel 1993). Both of them are detected by the goodness-of-fit tests, and then adapted models that take account of these kinds of heterogeneity can be fitted.

We used program MARK 4.0 (White & Burnham 1999) to model emigration and immigration. We considered several models for emigration, immigration and recapture probabilities. Emigration and immigration probabilities might have been time-dependent ( $\epsilon_t$ ,  $\iota_t$ ), constant across time ( $\epsilon$ ,  $\iota$ ), or gradually change over time (a linear

function of time) ( $\epsilon_T$ ,  $\iota_T$ ). Recapture probabilities were considered to be either constant across time ( $p$ ,  $r$ ), or time-dependent ( $p_t$ ,  $r_t$ ). Since we had no a priori expectations about the interaction between recapture and immigration or recapture and emigration we considered all possible combinations of these model fragments, resulting in a set of six different emigration and immigration candidate models. Because males and females of Cetti's Warblers differ in body measures recapture probabilities may differ among sex. Therefore we considered for this species additional recapture models which account for possible sex effects ( $p_{t \times \text{sex}}$ ,  $p_{t+\text{sex}}$ ,  $p_t$ ,  $p$ ;  $r_{t \times \text{sex}}$ ,  $r_{t+\text{sex}}$ ,  $r_t$ ,  $r$ ). Model selection was based on the small-sample-size adjusted Akaike's Information Criterion (AICc; Burnham & Anderson 1998). This statistic avoids under- and overfitting, and results in the selection of the most parsimonious model. Yet, because model selection may be ambiguous, we calculated model averaged values. They are calculated from the parameter estimates of each model, but weighed by the Akaike weight (Burnham & Anderson 1998). We used the program SODA (Schaub *et al.* 2001) to estimate the stopover duration. This estimation was done only for Reed Warblers, because it turned out that many individuals of the two other species were departing local breeding birds and estimates of stopover duration do not make sense then.

### Fuel deposition rate

We analysed data of recaptured birds with a linear regression model without an intercept to estimate the fuel deposition rate. The dependent variable was the body mass difference between the first and last capture, and the two main independent variables were the number of days between first and last capture ( $\Delta\text{day}$ ) and the number of hours between time of day at first and at last capture ( $\Delta\text{time}$ ). The estimated coefficients in this model are the averaged body mass increase between days (in  $\text{g day}^{-1}$ ) and the body mass increase within a day (in  $\text{g h}^{-1}$ ). Thus the model takes account of body mass changes within a day. The body mass increase between days is the fuel deposition rate.

For testing whether groups of birds (according to sex, age or moult status) differ in either the body mass increase between days or within days, these individual covariates are included in the model as interactions with the two main independent factors (see Schaub & Jenni 2000 for a detailed description of the model). Potential factors considered to explain variation of fuel deposition rates were the progress of season (all species), age (Moustached Warbler), moult (Moustached Warbler), sex (Cetti's Warbler) and year (Moustached and Cetti's Warbler).

To reduce possible effects of handling on fuel deposition rate, we only included recaptures that were more than one day after the capture. We only considered captures and recaptures of birds that were made within the period defined in Table 1. For Reed and Cetti's Warbler we only considered non-moulting individuals, as there were too few moulting individuals to make conclusive tests.

## RESULTS

### Immigration, emigration and stopover duration

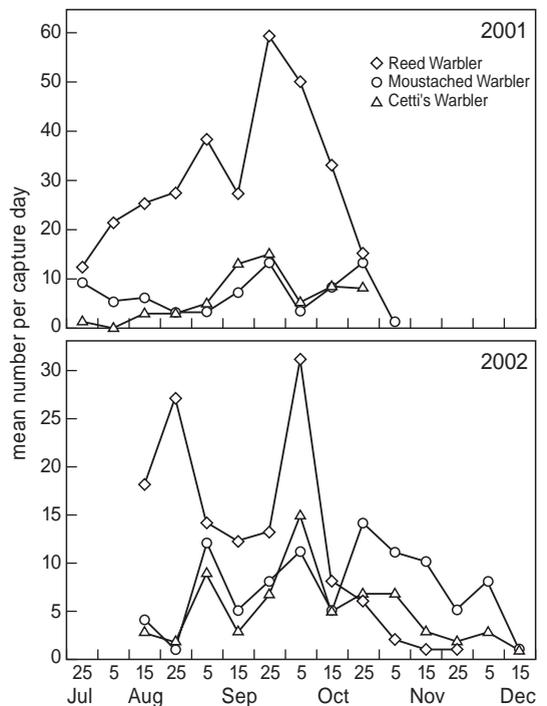
#### REED WARBLER

During autumn 2001 we captured 660 first-year individuals, and 157 in 2002 (Table 1). The migration lasted until the end of October and peaked in late September (Fig. 2). During autumn 2001, 41 individuals were recaptured at least once. In contrast, during autumn 2002 not a single individual was recaptured, hence emigration, immigration and fuel deposition rates could not be estimated for 2002.

The goodness-of-fit test of the model  $\{\epsilon_t, p_t\}$  did not indicate any heterogeneity ( $\chi^2_{10} = 2.47$ ,  $P = 0.99$ ). Modelling revealed that immigration and emigration probabilities were most likely a linear function of time (Table 2). However, the second best model with constant emigration probabilities had a similar AIC weight, hence the uncertainty about the linear trend was quite large. The model averaged weekly immigration and emigration probabilities were generally high, indicating a strong passage of birds. Immigration decreased

**Table 1.** Sample sizes (number of individual captured and recaptured) and time period considered for each of the three warbler species at Estagnol. 1y = first-year birds; ad = adults; M = males; F = females.

Species	Year	Time period	Number of	
			captures	recaptures
Reed Warbler	2001	25 July–31 Oct	1y 660	1y 41
	2002	15 Aug–23 Nov	1y 157	1y 0
Moustached Warbler	2001	25 July–08 Nov	1y 57	1y 13
			ad 80	ad 25
	2002	15 Aug–14 Dec	1y 37	1y 10
			ad 53	ad 12
Cetti's Warbler	2001	13 Aug–31 Oct	M 33	M 11
			F 69	F 16
	2002	15 Aug–07 Dec	M 20	M 6
			F 46	F 6



**Figure 2.** Mean number of captures per capture day of Reed, Moustached and Cetti's Warblers in different periods of 10 days in autumn 2001 and 2002 at Estagnol. All birds (captures and recaptures) are included.

during the season from 0.94 (95% confidence interval 0.73 – 0.99) at the end of July to 0.69 (0.47 – 0.85) at the end of October, and emigration from 0.89 (0.73 – 0.96) to 0.81 (0.66 – 0.90) during the same period. The stopover duration increased from 6.1 (3.0 – 9.2) days at the end of July to 11.1 days (7.6 – 14.7) at the end of October (Fig. 3).

MOUSTACHED WARBLER

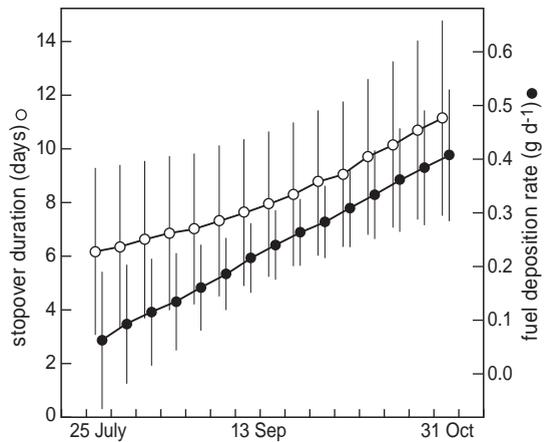
We caught 227 Moustached Warblers during the two autumns (Table 1). Individuals were captured until the end of the field work in mid-December and no clear migration peak was visible (Fig. 2). Sixty (26%) of these 227 birds were recaptured at least once. Since the intervals between capture occasions were not the same in both study years, we analysed the data for each year separately. The goodness of fit tests of the most complex models  $\{\epsilon_v, p_t\}$  indicated no significant heterogeneity (2001:  $\chi^2_{42} = 18.61, P = 0.99$ ; 2002:  $\chi^2_{34} = 12.33, P = 0.99$ ).

There was considerable model selection uncertainty for the immigration models in both years (Table 3). Model averaged immigration probabilities in 2001 varied over time in the range from 0.003 (95% confidence interval 0.00 – 0.36) to 0.34 (0.03 – 0.89) without an obvious trend over time (mean 0.08, 95% confidence interval 0.03 – 0.17). In autumn 2002 the model averaged weekly immigration probability decreased slightly from 0.14 (0.02 – 0.53) in mid-August to 0.06 (0.01 – 0.30) in mid-December.

Model selection for emigration revealed that emigration probabilities in both years were lower early in the season than later, and that recapture probability was constant (Table 3). In autumn 2001 weekly emigration probabilities were almost 0 in all time intervals apart from the last one in late October (0.85, 95% confidence interval: 0.42 – 0.98). The average weekly emigration probability over the whole period was 0.02 (0.00 – 0.38). In autumn 2002 when we sampled over a longer period, model averaged weekly emigration probability increased from 0.04 (0.00 – 0.32) in mid-August to 0.23 (0.03 – 0.74) in mid-December.

**Table 2.** Modelling immigration and emigration probabilities of first-year Reed Warblers at Estagnol in 2001. Given are the model, the deviance (Dev), the number of estimated parameters (Par), the difference of the small-sample-size adjusted AIC of the actual model and the best one ( $\Delta AICc$ ), and the Akaike weight. All six candidate models are listed.

Model	Dev	Par	$\Delta AICc$	Weight
<b>Immigration</b>				
$\iota_T, r$	38.90	3	0.00	0.82
$\iota_T, r_t$	16.55	16	4.42	0.09
$\iota, r_t$	18.78	15	4.57	0.01
$\iota_v, r$	24.27	15	10.06	0.00
$\iota, r$	51.53	2	10.62	0.00
$\iota_v, r_t$	6.83	25	13.88	0.00
<b>Emigration</b>				
$\epsilon_T, p$	33.33	3	0.00	0.60
$\epsilon, p$	36.16	2	0.81	0.40
$\epsilon, p_t$	19.59	15	10.94	0.00
$\epsilon_T, p_t$	17.69	16	11.13	0.00
$\epsilon_v, p$	24.24	15	15.59	0.00
$\epsilon_v, p_t$	7.55	24	18.00	0.00



**Figure 3.** Stopover duration and fuel deposition rate of first-year Reed Warbler during migration at Estagnol during autumn 2001. The vertical lines show 95% confidence intervals.

**Table 3.** Modelling immigration and emigration probabilities of Moustached Warblers at Estagnol. Given are the model, the deviance (Dev), the number of estimated parameters (Par), the difference of the small-sample-size adjusted AIC of the actual model and the best one ( $\Delta\text{AICc}$ ), and the Akaike weights. All six candidate models are listed.

2001					2002				
Model	Dev	Par	$\Delta\text{AICc}$	Weight	Model	Dev	Par	$\Delta\text{AICc}$	Weight
<b>Immigration</b>									
$\iota, r_t$	225.9	29	0.00	0.46	$\iota, r$	151.1	2	0.00	0.59
$\iota, r_t$	260.0	16	0.55	0.35	$\iota_T, r$	149.7	3	0.73	0.41
$\iota_T, r_t$	259.8	17	2.77	0.11	$\iota, r_t$	132.2	16	14.15	0.00
$\iota, r$	295.2	2	4.68	0.04	$\iota_T, r_t$	131.6	17	16.27	0.00
$\iota_T, r$	293.7	3	5.32	0.03	$\iota, r$	142.3	16	24.27	0.00
$\iota, r$	271.7	16	12.20	0.00	$\iota, r_t$	113.5	29	35.01	0.00
<b>Emigration</b>									
$\varepsilon_T, p$	264.8	3	0.00	0.92	$\varepsilon_T, p$	147.8	3	0.00	0.58
$\varepsilon, p_t$	241.1	16	6.21	0.04	$\varepsilon, p$	150.6	2	0.66	0.42
$\varepsilon_T, p_t$	241.0	17	7.52	0.02	$\varepsilon, p_t$	141.3	16	24.41	0.00
$\varepsilon, p$	274.7	2	7.76	0.02	$\varepsilon_T, p_t$	140.1	17	25.98	0.00
$\varepsilon, p$	262.3	16	26.39	0.00	$\varepsilon, p$	145.0	16	28.11	0.00
$\varepsilon, p_t$	238.7	29	36.42	0.00	$\varepsilon, p_t$	138.2	29	61.07	0.00

#### CETTI'S WARBLER

We captured 168 Cetti's Warbler of known sex (68% females) during the two autumns, of which 39 individuals have been recaptured at least once (Table 1). As in the Moustached Warbler, individuals were captured until the end of the field work in mid-December and no clear migration peak was visible (Fig. 2). The most complex model considered sex and time-dependence  $\{\varepsilon_{\text{sex}^*t}, p_{\text{sex}^*t}\}$  and fitted the data (2001:  $\chi^2_{45} = 19.07$ ,  $P = 0.99$ ; 2002:  $\chi^2_{29} = 9.64$ ,  $P = 0.99$ ). However, the directional tests in U-CARE indicated that there was a significant proportion of transients in year 2001 (males:  $z = 1.64$ ,  $P_{\text{one tailed}} < 0.05$ ; females:  $z = 1.86$ ,  $P_{\text{one tailed}} = 0.03$ ), but not in 2002 (males:  $z = 1.05$ ,  $P_{\text{one tailed}} = 0.15$ ; females: not computable). For the year 2001 we therefore formulated emigration models that took account of transients (Pradel *et al.* 1997, Schaub *et al.* 2004). Immigration models can not be fitted when transients occur, because information about capture probability of the transients is missing (Nichols *et al.* 2000). For year 2001, the most complex struc-

ture for emigration models assumed that the proportion of transients among newly caught Cetti's Warblers ( $\tau$ ) as well as emigration probabilities, were either constant ( $\tau, \varepsilon$ ), time-dependent ( $\tau_t, \varepsilon_t$ ) or a linear function of time ( $\tau_T, \varepsilon_T$ ). For 2002, when no significant proportion of transients occurred, we fitted the same models as in the other species, but considered possible sex-specific recapture probabilities.

Modelling immigration probability in 2002 revealed that recapture probability differed among sexes and that immigration probability possibly had a seasonal trend (Table 4). The model averaged weekly immigration probability was not very high, it decreased from 0.14 (95% confidence interval 0.02 – 0.61) in mid-August to 0.05 (0.01 – 0.33) at the beginning of December.

Modelling emigration probability of Cetti's Warblers in autumn 2001 revealed that model selection uncertainty was considerable (Table 4). The model averaged emigration probabilities increased during the season from 0.08 (0.02 – 0.34) in mid-August to 0.22 (0.03 – 0.69) at the

**Table 4.** Modelling immigration and emigration probabilities of Cetti's Warblers at Estagnol. Given are the model, the deviance (Dev), the number of estimated parameters (Par), the difference of the small-sample-size adjusted AIC of the actual model and the best one ( $\Delta$ AICc), and the Akaike weights. The five best and the most complicated models are listed.

2001					2002				
Model	Dev	Par	$\Delta$ AICc	Weight	Model	Dev	Par	$\Delta$ AICc	Weight
<b>Immigration</b>									
-	-	-	-	-	$l, r_{sex}$	116.4	3	0.00	0.60
-	-	-	-	-	$l_T, r_{sex}$	115.0	4	0.88	0.39
-	-	-	-	-	$l, r$	128.5	2	9.98	0.00
-	-	-	-	-	$l_T, r$	127.6	3	11.23	0.00
-	-	-	-	-	$l_t, r_{sex}$	106.2	17	26.30	0.00
-	-	-	-	-	$l_{sex^*t}, r_{sex^*t}$	83.2	57	294.94	0.00
<b>Emigration</b>									
$\tau_T, \varepsilon_T, p_t$	159.1	15	0.00	0.28	$\varepsilon, p_{sex}$	121.4	3	0.00	0.61
$\tau, \varepsilon, p_{sex+t}$	162.0	14	0.37	0.24	$\varepsilon_T, p_{sex}$	120.3	4	1.04	0.36
$\tau, \varepsilon, p_t$	164.8	13	0.75	0.20	$\varepsilon_T, p_t$	130.0	3	8.59	0.01
$\tau_T, \varepsilon_T, p_{sex+t}$	157.4	16	0.77	0.19	$\varepsilon, p$	132.2	2	8.60	0.01
$\tau_T, \varepsilon_T, p_{sex}$	182.5	6	2.31	0.09	$\varepsilon, p_{sex^*t}$	107.9	13	11.26	0.00
$\tau_{sex^*t}, \varepsilon_{sex^*t}, p_{sex^*t}$	115.9	62	141.21	0.00	$\varepsilon_{sex^*t}, p_{sex^*t}$	88.9	56	293.34	0.00

end of October. In autumn 2002 the model selection for the emigration was similarly ambiguous, as the two models with and without a seasonal trend had similar support by the data (Table 4). All models with sex-specific recapture probabilities were well supported. The model averaged weekly emigration probability were similar to the previous year, they increased from 0.08 (0.02 – 0.30) in mid-August to 0.17 (0.03 – 0.53) in early December.

When a sex difference in recapture probabilities in these 3 data sets was apparent, it appeared that recapture probabilities of males were always higher than that of females.

### Fuel deposition rate

The regression analysis (Table 5) showed that Reed Warblers significantly increased body mass. The fuel deposition rate increased in the course of the season (Fig. 3), at the peak of migration (end of September) it was 0.29 (SE 0.035) g day<sup>-1</sup>. The lean body mass at Estagnol was 10.2 g (mean body mass of Reed Warblers without visible fat),

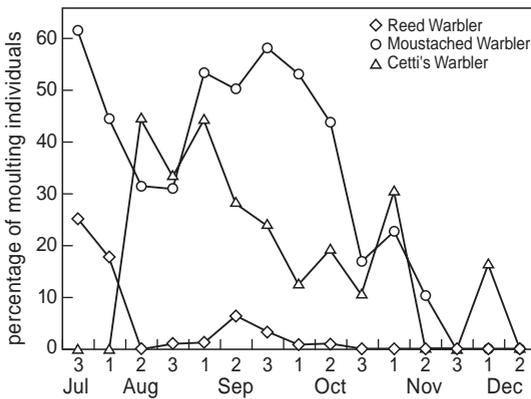
hence the fuel deposition rate was 2.85% per day at the peak of migration. Combined with the estimated stopover duration and assuming a constant fuel deposition rate during their stay, Reed Warblers gained 0.37 g of body mass in late July and 4.48 g in late October. Irrespective of moult, sex or age the body mass of Moustached and the Cetti's Warbler did not change significantly during the study period in both years (Table 5).

### Moult

Very few Reed Warblers with active body feather moult were caught in Estagnol (3.2% of all individuals in active moult,  $n = 824$ ; Fig. 4). The most individuals in active moult occurred in late July and early August, later there were only very few. The proportion of Moustached Warbler in moult was 33.9% ( $n = 251$ ), peaked in late July and September (Fig. 4), and did not differ among age classes (adults: 36.0%,  $n = 150$ ; first-year birds: 30.6%,  $n = 101$ ;  $\chi^2_1 = 0.76$ ,  $P = 0.38$ ). Some of the moulting individuals were not only moulting

**Table 5.** Summary of modelling the fuel deposition rate of three warbler species at Estagnol. The dependent variable in the model is the body mass difference between first and last capture. Given are degrees of freedom (*df*), sums of squares (SS), variance ratio (*F*). \*\*  $P < 0.001$ , \*  $P < 0.01$ .

Source	Reed Warbler ( <i>n</i> = 44)			Moustached Warbler ( <i>n</i> = 52)			Cetti's Warbler ( <i>n</i> = 27)		
	<i>df</i>	SS	<i>F</i>	<i>df</i>	SS	<i>F</i>	<i>df</i>	SS	<i>F</i>
$\Delta$ date	1	176.96	65.24**	1	0.18	0.29	1	1.38	2.34
$\Delta$ time	1	1.79	0.65	1	0.01	0.02	1	1.86	3.15
$\Delta$ date $\times$ age	-	-	-	1	1.72	2.80	-	-	-
$\Delta$ time $\times$ age	-	-	-	1	0.37	0.60	-	-	-
$\Delta$ date $\times$ moult	-	-	-	1	1.81	2.95	-	-	-
$\Delta$ time $\times$ moult	-	-	-	1	0.10	0.16	-	-	-
$\Delta$ date $\times$ sex	-	-	-	-	-	-	1	0.12	0.20
$\Delta$ time $\times$ sex	-	-	-	-	-	-	1	0.14	0.23
$\Delta$ date $\times$ date	1	25.08	9.25*	1	0.37	0.61	1	0.39	0.66
$\Delta$ time $\times$ date	1	0.42	0.16	1	0.01	0.01	1	0.87	1.47
$\Delta$ date $\times$ year	-	-	-	1	0.33	0.54	1	0.03	0.05
$\Delta$ time $\times$ year	-	-	-	1	0.05	0.09	1	0.19	0.32
Error	40	108.50		42	25.80		19	11.26	



**Figure 4.** Proportion of captured Reed Warblers ( $n = 897$ ), Moustached Warblers ( $n = 334$ ) and Cetti's Warbler ( $n = 262$ ) that were mouling in different periods of 10 days at Estagnol (pooled data from autumn 2001 and 2002).

body feathers but also remiges (14.7% of all captures,  $n = 251$ ). Again, there was no difference in the proportion of birds in active wing moult among age classes (adults: 14.0%,  $n = 150$ ; first-

year birds: 15.8%,  $n = 101$ ;  $\chi^2_1 = 0.16$ ,  $P = 0.69$ ). The proportion of Cetti's Warbler in active body feather moult was lower than in Moustached Warbler (20.5% of all captures,  $n = 190$ ;  $\chi^2_1 = 9.52$ ,  $P < 0.05$ ) and decreased in the course of the autumn (Fig. 4). Active wing feather moult was never observed in Reed and Cetti's Warblers.

## DISCUSSION

We found that long-distance migrant Reed Warblers stayed on average less than 10 days at Estagnol, significantly increased body mass during stopover and had already completed moult at the time of passage. In contrast, there were few emigrating and immigrating individuals among the two short-distance migrants Moustached and Cetti's Warblers, pointing towards a high stopover duration during which they did not change body mass and many were mouling. The Cetti's Warbler only moulted body feathers whereas Moustached Warblers moulted in addition remiges.

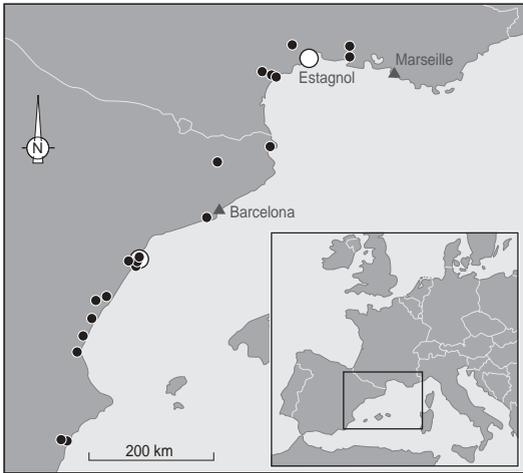
The results of this study fit nicely within the proposed migration strategy of Reed Warblers. According to current knowledge (Herremans 1990, Schaub & Jenni 2000a, b, 2001) we expected that fuel deposition at Mediterranean sites should be high but stopover duration not different from other sites in central Europe. Indeed, the fuel deposition rate at Estagnol ( $0.29 \text{ g day}^{-1}$ ) was even higher compared to fuel deposition rates at other Mediterranean stopover places (Algeria:  $0.25 \text{ g day}^{-1}$  (Bairlein 1988), northern Spain:  $0.10 \text{ g day}^{-1}$ , southern Spain:  $0.16 \text{ g day}^{-1}$ , northern Morocco:  $0.26 \text{ g day}^{-1}$  (Schaub & Jenni 2000a)). Furthermore, average stopover duration of non-moulting Reed Warblers at Estagnol (8.5 days) was similar to stopover duration at different stopover places along the migration route (9.5 days). Reed Warblers at Estagnol increased through autumn their speed of fuel deposition and stopover duration, resulting in increasing body mass gain. The potential flight range of Reed Warblers migrating later in the season is therefore significantly longer than that of the early migrants, which enable them to conduct longer migratory flight steps. Although the stopover duration is longer at the end of the season, the longer potential flight range may enable them to achieve a higher migration speed. These findings refer to first-year Reed Warblers, the migration strategy of adults remains to be studied when more data are available.

The migration strategies of the two short-distance migrants turned out to be similar. We found that emigration and immigration probabilities were significantly lower than that of the Reed Warblers, indicating little passage of Moustached and Cetti's Warbler at Estagnol and a long stopover duration of the present individuals. In the course of the season immigration probabilities slightly decreased while emigration probabilities slightly increased. This indicates that arrival of non-local individuals occurred early in the season and that departure of individuals occurred late. In contrast to the long-distance migrant Reed Warbler, the two short-distance migrants did not significantly accumulate fuel stores. This was con-

sistent among the different groups of birds (age classes, sex, moult status) and did not change in the course of the season. Because the two species did not accumulate significant amounts of fuel stores they were able to conduct only short migratory flights. A significant proportion of both species was moulting during stopover at Estagnol, the Cetti's Warbler conducted a partial moult while adult and first-year Moustached Warbler conducted a complete moult. Finding out why the moulting strategy of these two species differs would require more detailed studies. Based on these results and considering ring recoveries we derive the following proposals about where Moustached and Cetti's Warblers present at Estagnol originate and where they winter.

The low immigration probability of Moustached Warbler indicates that many individuals were already present at Estagnol at the time when the study started (likely local breeding birds), still a fraction of birds originate from other areas. Despite the recovery of one individual in southern Hungary in July 2003 that we ringed at Estagnol in November 2002, it is unlikely that most immigrating Moustached Warblers originate from eastern Europe. If it would be a common pattern, we would have expected to get more recoveries given the relatively high ringing effort in southern France (2487 birds ringed from 1993 to 2002) and in eastern Austria (3998 birds ringed from 1974 to 1983, Berthold *et al.* 1991). Rather it is likely that most passing individuals originate from breeding sites near Estagnol, because only very few individuals with significant fuel stores have been captured. From the end of October to mid-December, emigration increases and numbers of captures tend to decrease. Most of the birds breeding in the French Mediterranean area winter in Spain, as evidenced by numerous ring recoveries (Fig. 5). The distance between Estagnol and these possible wintering sites is relatively short (about 200–400 km) and could thus be covered without significant energy stores. The resources provided in autumn at Estagnol are hence mainly used for moulting.

Ring recoveries of Cetti's Warbler ringed or recovered in France indicate that the species is



**Figure 5.** Recoveries of Moustached Warblers in the western Mediterranean area (1983–2003). The dots are ringing sites of birds either ringed in France and recovered in Spain (59 birds ringed from March to November) or ringed in Spain and recovered in France (26 birds ringed from October to February). The open large circles indicate the study site (Estagnol) and the Ebro delta where one bird ringed at Estagnol was recovered.

almost completely sedentary: only 0.9% ( $n = 3329$  recoveries) were recovered at a longer distance than 10 km from the ringing place (data provided by the National Museum of Natural History, Paris). Because of the short migratory distances and the fact that Cetti's Warbler do not breed in the reed bed at Estagnol, it is likely that the individuals captured at Estagnol originate from river banks where they breed but not winter (personal unpublished data) and from bushes surrounding the study site. After breeding they move from these habitats into the reed bed for moulting. Thereafter they mainly leave the reed bed again and spend the winter along the Mediterranean coast in bushes surrounding wetlands (two birds ringed at Estagnol have been recovered in winter at 5 km). 68% of the Cetti's Warblers captured were females despite the fact that their capture probability was lower than that of males. It indicates that females were significantly more abundant at Estagnol than males. This result is consis-

tent with observations from another reed bed in the Camargue where an influx of females was found in August to October (Isenmann 1993). We can only speculate about migratory movements of the males. It is likely that they are mainly sedentary or that they use different habitats during migration. Sex-related differential migration and habitat segregation has been found in other short-distance migrants as well (Alerstam 1994, Catry *et al.* 2004).

Using individual based capture-recapture data we showed that the stopover ecology in terms of stopover duration, fuel deposition and moult strongly differed between a long-distance and two partial short-distance migrants. In order to get a more detailed understanding about these interspecific differences it would be promising to study food selection and the spatio-temporal pattern of food availability.

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## SAMENVATTING

Veel Europese zangvogels zijn langeafstandstrekkingers, die elk jaar tussen Europa en Afrika heen en weer pendelen. Korte periodes van vliegen worden dan afgewisseld met veel langere periodes waarin gegeten wordt om energie op te doen voor het volgende traject. Er zijn ook soorten die minder grote afstanden afleggen, en dus ook minder reserves behoeven aan te leggen. In deze studie wordt een vergelijking gemaakt in trekgedrag tussen een drietal verwante zangers: de Kleine Karekiet *Acrocephalus scirpaceus*, Zwartkoprietzanger *A. melanopogon*, en de Cetti's Zanger *Cettia cetti*. Het onderzoeksgebied lag in Zuid-Frankrijk, vlak bij de Middellandse Zee. De vogels werden in het najaar gevangen met mistnetten, waarna ze werden geringd, gemeten en gewogen. Door intensief te vangen en te ringen werden veel vogels teruggevangen.

Zo kon de gewichtstoename berekend worden, dat wil zeggen de snelheid waarmee vogels energiereserves voor de trek aanlegden. Bovendien boden de ringwaarnemingen de mogelijkheid om met geavanceerde rekenmodellen de sterkte van de doortrek te bepalen. Zo werd de mate van immigratie in het studiegebied berekend, evenals de emigratie en verblijfsduur. Van de Kleine Karekiet werden vooral eerstejaars vogels gevangen en nauwelijks adulte vogels. De gemiddelde verblijfsduur van de Kleine Karekiet in het onderzoeksgebied was 8,5 dagen, oplopend van 6,1 eind juli tot 11,1 eind oktober. Deze snelheid van doortrek is vergelijkbaar met wat elders in Europa is vastgesteld. De gewichtstoename (vooral door opslag van vet) was 0,29 g per dag tijdens de piek van de trek eind september. Hiermee springt dit gebied er gunstig uit in vergelijking met andere plekken rond de Middellandse Zee, waar de vogels beduidend minder snel vet opslaan. In de loop van het najaar namen de karekieten sneller in gewicht toe, en omdat ze bovendien langer bleven, nam de opslag van lichaamsreserves toe van 0,37 g in juli tot 4,48 g eind oktober. Dit wijst erop dat het trekpatroon sterk verschilt tussen vroege en late doortrekkers, omdat late vogels een veel groter bereik hebben dan vogels die eerder doortrekken. Zwartkoprietzangers bleken vooral vogels afkomstig uit het achterland van de vangplek. Veel vogels kwamen naar het vanggebied om te ruïen. De gewichtstoename was gering, en hoewel de meeste vogels laat in het najaar wegtrokken, was de trekafstand klein, enkele honderden kilometers tot in Spanje. Cetti's zanger zijn amper trekvogel te noemen. De gevangen vogels waren afkomstig uit struikgewas dat het studiegebied omringde, en de meeste dieren bleven binnen 5 km van de vangplek. In hoeverre de verschillen in trekpatroon tussen de bestudeerde zangvogels te maken heeft met voedselaanbod en -keuze wordt nu onderzocht. (JP)

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