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Stopover durations of three warbler species along their autumn migration route

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Abstract In migrating birds, the success of migration is determined by stopover duration, the most important factor determining overall speed of migration, and fuel deposition rate. However, very little is known about stopover durations of small migrant birds, because appropriate methods for data analysis were lacking until recently. We used a new capture-recapture analysis to estimate stopover durations of 1st-year reed warblers *Acrocephalus scirpaceus*, sedge warblers *A. schoenobaenus* and garden warblers *Sylvia borin* at 17 stopover sites in Europe and Africa during autumn. Average stopover duration of non-moulting reed warblers was 9.5 days while moulting conspecifics stayed about twice as long. Average stopover duration of sedge warblers was 9.1 days and, in contrast to the other two species, differed between years at several sites. Garden warblers stayed 7.7 days on average. The long stopover duration of the reed warbler, resulting in slow overall migration speed, is related to its low fuel deposition rate. It can be explained by low, but predictable, food resources and an early departure during moult. Compared to the reed warbler, the stopover duration of the sedge warbler varies more between sites and probably also between years, as the supply of its preferred diet (reed aphids) is spatially and temporally unpredictable but can be superabundant. The short stopover duration of the garden warbler, leading to high overall migration speed, can be related to high fuel deposition rates, probably brought about by a change to an abundant, predictable and long-lasting fruit diet. Within species, stopover duration did not change

significantly along the migration route. Hence, an increase of migration speed along the migration route, as suggested in the literature, may be caused by longer flight bouts in the south. However, it remains largely unknown which environmental and possibly endogenous factors regulate stopover duration.

Keywords Stopover length · Migration strategy · Passerine birds · Capture-recapture · Cormack-Jolly-Seber models

Introduction

Birds usually divide their migration between the breeding and the wintering grounds into phases of flights and stopovers. At good stopover sites, energy reserves are replenished to be used partly or completely during the next flight bout. The distance may be covered in several small or a few long flight bouts. The organisation of the journey in flight bouts and stopovers is likely to depend on the availability and quality of potential stopover sites, on short-term environmental factors and on various selection pressures, as predicted by theoretical models (Alerstam and Lindström 1990; Weber et al. 1994, 1998b). However, empirical data on the organisation of migration along entire migration routes are scarce and, hence, also tests of predictions from the theoretical models.

The main elements of migration organisation are length of flight bout, stopover duration and fuel deposition rate. These elements are interrelated because a flight bout can only be covered if the required energy stores have previously been accumulated and this depends on fuel deposition rate and stopover duration. Many long-distance migrants seem to be under selective pressure to minimise time spent migrating (Ellegren 1991; Lindström and Alerstam 1992; Klaassen and Lindström 1996; Fransson 1998). Hence stopover duration, which is by far the most important factor determining overall speed of migration, and fuel deposition rate are decisive for the success of migration.

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Fuel deposition rates are comparatively easy to estimate by following the change in body mass or fat stores of individuals at a stopover site (e.g. Schaub and Jenni 2000a) or by measuring the concentration of certain metabolites in the plasma (Jenni-Eiermann and Jenni 1994). In contrast, empirical data on stopover duration are much more difficult to obtain (Kaiser 1999). While large birds can be tracked by satellites, telemetry cannot be applied to small birds over large distances. In small birds, capture-recapture data are widely sampled at stopover sites and contain all the information about stopover duration. However, until recently stopover duration was estimated in most studies by calculating minimum stopover duration (the time elapsed between first and last capture; e.g. Cherry 1982; Morris et al. 1996) or, in some studies, with Jolly-Seber models (e.g. Kaiser 1995) or derivatives thereof (e.g. Lavee et al. 1991) which provide estimates of the probabilities of staying at the site after capture. While minimum stopover duration is inappropriate for various reasons, neither method estimates the time the birds stayed at the site before capture (see Schaub et al. 2001). Consequently, stopover duration has generally been underestimated, and there exist hardly any reliable estimates of stopover duration for small migrants and information on the influence of environmental factors. Recently, a method has been developed which combines a survival and recruitment analysis for estimating stopover duration before and after capture (total stopover duration; Schaub et al. 2001). This allows reliable estimation of stopover duration and testing for differences between groups of birds and for influencing factors.

In this study, we estimate stopover duration of 1st-year birds for three species of long-distance migrant passerines at various sites along their migration route from northern Europe to North Africa with this new method. The three species with breeding areas in northern and central Europe and wintering grounds in sub-Saharan Africa are similar in timing and route of migration, but differ in timing of moult, food preferences and availability of food.

While garden warblers (*Sylvia borin*) and sedge warblers (*Acrocephalus schoenobaenus*) generally moult before and after migration, respectively (Berthold et al. 1972; Redfern and Alker 1996), the reed warbler (*A. scirpaceus*) terminates moult while migrating over northern and central Europe (Herremans 1990; Schaub and Jenni 2000a). The fuel deposition rate of moulting reed warblers is extremely low (Schaub and Jenni 2000a), probably because moult is energy-demanding. Hence, it is likely that the stopover duration at this stage is long, because it takes a long time for enough fuel to be deposited to cover the energy expenditure of the next flight bout. We therefore tested whether moulting and non-moulting reed warblers differed in stopover duration.

Reed warblers feed opportunistically on insects (Bibby and Green 1981), sedge warblers mainly on reed aphids (Bibby and Green 1981) and garden warblers on a mixed diet containing insects and fruits (Simons and Bairlein 1990). The food resources are likely to be rather

constant between years for reed and garden warblers, but highly variable between sites and years (Hanski and Woiwod 1993) for sedge warblers, as they depend on a superabundance of reed aphids for extensive fat deposition (Bibby and Green 1981). We therefore tested whether stopover duration differs between years. If birds adjust their stopover duration according to food availability, we would expect stopover duration of the sedge warbler to be much more variable between years and sites than in reed and garden warblers.

Given the differences in moult strategy, food preferences and availability, we compare stopover duration along the migration route between the three species. We further related these differences in stopover duration to the overall speed of migration (including stopovers) and to the increase of overall migration speed along the migration route that was proposed from recoveries of ringed birds.

Finally, from the pattern of stopover durations along the migration route, from data on moult, fuel deposition rate and body mass collected within the same project (Schaub and Jenni 2000a, 2000b) and from literature data on moult, habitat and food, we derive a characterisation of the organisation of the autumn migration of the three species.

Materials and methods

Sites and data sampling

Most data used in this study were the product of a collaboration among ringing stations during 1994–1996 within a network funded by the European Science Foundation (Bairlein 1997). Out of 39 participating ringing stations, 17 provided enough data for the analysis of stopover duration of at least one of the three species reed warbler, sedge warbler and garden warbler (Table 1, Fig. 1).

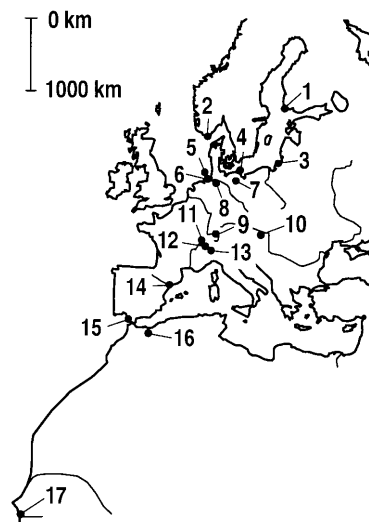


Fig. 1 Location of ringing sites (1 Rauvola, 2 Lista, 3 Rybachy, 4 Greifswalder Oie, 5 Helgoland, 6 Oldeog, 7 Galenbecker See, 8 Reit, 9 Mettnau, 10 Illmitz, 11 Portalban, 12 Gröne, 13 Bolle di Magadino, 14 Ebro Delta, 15 Coto de Doñana, 16 Oued Moulouya, 17 Ginak)

Table 1 Location of ringing sites, operating years and study period to which the analyses refer. The site numbers correspond to those in Fig. 1

Site	Country	Coordinates	Operating years	Study period		
				Reed warbler	Sedge warbler	Garden warbler
1. Rauvola	Finland	60.4°N 22.3°E	1994–1996	4 Aug–27 Sep	30 Jul–2 Oct	9 Aug–17 Sep
2. Lista	Norway	58.1°N 6.6°E	1994–1996	4 Aug–17 Oct	30 Jul–7 Oct	–
3. Rybachy	Russia	55.2°N 20.8°E	1994–1996	4 Aug–12 Oct	30 Jul–2 Oct	4 Aug–7 Oct
4. Greifswalder Oie	Germany	54.3°N 13.9°E	1995–1996	–	–	14 Aug–2 Oct
5. Helgoland	Germany	54.2°N 7.9°E	1995–1996	–	–	14 Aug–21 Sep
6. Oldeog	Germany	53.8°N 8.0°E	1994–1996	–	–	9 Aug–25 Sep
7. Galenbecker See	Germany	53.6°N 13.7°E	1994–1996	4 Aug–7 Oct	4 Aug–8 Sep	4 Aug–22 Sep
8. Reit	Germany	53.5°N 10.1°E	1995	4 Aug–7 Oct	–	–
9. Mettnau	Germany	47.7°N 9.0°E	1995–1996	9 Aug–12 Oct	–	4 Aug–27 Sep
10. Illmitz	Austria	47.5°N 18.5°E	1974–1983, 1989–1993	–	4 Aug–7 Oct	–
11. Portalban	Switzerland	46.9°N 6.9°E	1987–1989	9 Aug–22 Oct	–	9 Aug–2 Oct
12. Grône	Switzerland	46.3°N 7.4°E	1985	14 Aug–12 Oct	–	–
13. Bolle di Magadino	Switzerland	46.2°N 8.9°E	1994–1996	14 Aug–27 Oct	4 Aug–7 Oct	–
14. Ebro Delta	Spain	40.4°N 0.5°E	1995–1996	24 Aug–6 Nov	–	–
15. Coto de Doñana	Spain	37.2°N 6.5°W	1994–1996	3 Sep–27 Oct	–	29 Aug–27 Oct
16. Oued Moulouya	Morocco	34.1°N 2.5°E	1994, 1996	24 Aug–27 Oct	–	–
17. Ginak	Gambia	13.5°N 16.7°W	1995–1996	–	–	3 Oct–21 Nov

All ringing stations were requested to collect data in a standardised way (Bairlein 1995), which included daily ringing from dawn to dusk. Most stations provided data for the period 1994–1996, but in Portalban, Grône and Illmitz data were also collected in the same way in earlier years. Every bird captured was individually marked with a ring and aged (Jenni and Winkler 1994). Date of capture and intensity of body feather moult (three levels: no feathers growing; 1–20 feathers growing; more than 20 feathers growing) were recorded. The birds were released immediately after this procedure. Recaptures were treated in an analogous way.

We considered 1st-year birds which were first captured within the period of main passage given in Table 1. Hence, for reasons of data structure, some early and late migrants were excluded. Birds with fewer than 20 growing feathers were classified as non-moulting birds and the others as moulting ones. Due to the species-specific moulting patterns the data set comprises only non-moulting sedge and garden warblers but both non-moulting and moulting reed warblers.

Estimation of stopover duration

The estimation of stopover duration is based on a new method described in detail elsewhere (Schaub et al. 2001), and we only outline the general principle here. We analysed the capture-recapture data for each site and species with Cormack-Jolly-Seber models which allow separation of the recapture rate (p) from the local survival rate (ϕ) and from the recruitment rate (γ), respectively. We estimated for birds that were present at the site at time i , the probabilities of having already been at the site at time $i-1$ (equivalent to the probability of not having immigrated between $i-1$ and i) by means of a recruitment analysis (Pradel 1996) and the probability of still being at the site at time $i+1$ (equivalent to the probability of not having emigrated between i and $i+1$) by means of a survival analysis (Lebreton et al. 1992). These probabilities were converted into an estimated time spent by the birds at the site before and after time i . The sum of the two parts is the total stopover duration.

Analyses of recruitment and survival were based on the individual capture histories (including birds caught only once) which were pooled over 5 days. Pooling reduces the number of parameters to estimate and thus the likelihood of estimating all of them is increased. However, pooling introduces a bias in the parameter estimates of more than 5% if the degree of pooling is high and capture and recruitment/survival probabilities are low (Hargrove and Borland 1994), which was not the case in our data sets.

Capture-mark-recapture statistics require several assumptions to be met (Lebreton et al. 1992; Cooch et al. 1997) which can be tested by goodness-of-fit tests. Therefore, we first assessed the goodness-of-fit of a global Cormack-Jolly-Seber model with the program REL-CR, a modified version of RELEASE (Burnham et al. 1987) and then evaluated which of the candidate models fitted the data best. If the deviation from the Cormack-Jolly-Seber model was significant we examined the four subtests provided by REL-CR. These tests are particularly useful for obtaining indications of possible reasons for significant test statistics. For example, if there is a significant part of birds in the population that behaves as transients, the contingency tables of subtest 3SR are all biased in the same way (Pradel et al. 1997). Similarly, immediate trap-shyness or trap-happiness of a significant proportion of birds after first capture can be detected by inspecting the subtest 2Ct (Pradel 1993). If a lack of fit was observed in some years but not in others, we deleted the years with significant lack of fit and continued with the remaining data. Lack of fit might also occur if the probability of staying at the site depends on the time the birds have spent at the site already. Such a phenomenon is not easy to detect, because all subtests might be influenced, but the most severe case (transients) is easily detectable. A further reason for the lack of fit is extra-multinomial variation in the data, a phenomenon that is quite common with multinomial data (Lebreton et al. 1992; Cooch et al. 1997). A biological reason for extra-multinomial variation in the data (overdispersion) is a lack of independence between individuals, which is likely if birds migrate in groups. A non-biological reason is heterogeneity in survival or capture probability between individuals. In the presence of overdispersion estimates of model parameters remain unbiased, but their variance is underestimated (McCullagh and Nelder 1989). Therefore, overdispersion has to be taken into account in model selection and estimation of the variance (Anderson et al. 1994). As an estimate of the degree of overdispersion, we calculated the variance inflation factor \hat{c} as the quotient of the residual deviance and the residual degrees of freedom from the goodness-of-fit test (Burnham and Anderson 1998). We calculated \hat{c} up to a significance level of $P=0.10$ of the goodness-of-fit tests; beyond 0.10 it was assumed to be 1.

For the recruitment and survival analyses we fitted predefined models to the data with the program SURGE (Reboullet et al. 1999). For each model we calculated the modified Akaike information criterion (QAIC_c), which accounts for overdispersion and sample size (Burnham and Anderson 1998). The model with the smallest QAIC_c value was chosen to make inferences and to estimate stopover duration.

Table 2 Candidate models, model notation and biological significance. γ denotes recruitment probability (stopover duration before capture), ϕ survival probability (stopover duration after capture), p recapture probability, m moult intensity class, y year, t time

Species	Model	Significance
Reed warbler	$\gamma_{m^*y}/\phi_{m^*y}, P_{m^*y^*t}$	Recruitment and survival probabilities differ according to moult and year, recapture probability differs according to moult, year and time
	$\gamma_{m^*y}/\phi_{m^*y}, P_{m^*y}$	Recruitment, survival and recapture probabilities differ according to moult and year
	$\gamma_{m^*}/\phi_{m^*}, P_{m^*t}$	Recruitment and survival probabilities differ according to moult, recapture probability differs according to year and time
	$\gamma_{m^*}/\phi_{m^*}, P_m$	Recruitment, survival and recapture probabilities differ according to moult
	$\gamma_y/\phi_y, P_{y^*t}$	Recruitment and survival probabilities differ according to year, recapture probability differs according to year and time
	$\gamma_y/\phi_y, P_y$	Recruitment, survival and recapture probabilities differ according to year
Sedge and garden warblers	$\gamma/\phi, P_t$	Recruitment and survival probabilities are constant, recapture probability differs according to time
	$\gamma/\phi, p$	Recruitment, survival and recapture probabilities are constant
	$\gamma_y/\phi_y, P_{y^*t}$	Recruitment and survival probabilities differ according to year, recapture probability differs according to year and time
	$\gamma_y/\phi_y, P_y$	Recruitment, survival and recapture probabilities differ according to year
	$\gamma/\phi, P_t$	Recruitment and survival probabilities are constant, recapture probability differs according to time
	$\gamma/\phi, p$	Recruitment, survival and recapture probabilities are constant

Our intention was to obtain a single estimate of stopover duration for the entire study period of each site and we therefore considered no candidate models with seasonal variation in the local survival and the recruitment rates (Table 2). However, in order to obtain estimates of stopover duration that were as precise as possible, we included models with time-dependent recapture probabilities.

Once the best model for stopover duration before capture and the best model for stopover duration after capture had been identified, we calculated total stopover duration and its precision by a non-parametric bootstrap procedure with program soda (available at <ftp://ftp.cefe.cnrs-mop.fr/pub/biom/soft-CR/>). Increasing the number of resamplings in the bootstrap had no effect on the estimation of the mean, but decreased its precision slightly. The mean of a typical data set ($n=567$) and its 95% confidence interval limits were 12.26 (9.45–15.77) with 1,000 resamplings and 12.25 (9.35–15.88) with 10,000 resamplings. We therefore ran only bootstraps with 1,000 resamplings. At this stage, bootstrapping is not possible for additive model structures and for models that have group effects on the survival/recruitment parameter structure with no group effects on the recapture parameter structure, or vice versa. This reduced the number of models considered (Table 2).

Results

Stopover duration of reed warblers

Goodness-of-fit tests of Cormack-Jolly-Seber models were significant for the data sets from 6 out of 12 sites. The significant test results from Portalban ($\chi^2_{125}=161.4$, $P<0.05$), the Ebro Delta ($\chi^2_{81}=168.0$, $P<0.001$) and from the Coto de Doñana ($\chi^2_{37}=88.9$, $P<0.001$) could be attributed to the occurrence of a considerable proportion of transients in some years (Portalban in 1988; Ebro Delta in 1996; Coto de Doñana in 1994 and 1995). For Lista, the model did not fit the data (model and data were significantly different, $\chi^2_{60}=87.4$, $P<0.05$), due to capture heterogeneity in the year 1995. Therefore, we omitted these years for the calculation of stopover duration. The goodness-of-fit tests without these years were no longer

(5-day period). Note that the notation is similar to that of general linear models. Hence a model denoted as a^*b contains the two main effects a and b and the interaction between a and b

significant (Table 3), except for the reed warblers at the Ebro Delta in 1995. For this and the two other sites with significant goodness-of-fit tests, we found no indications of the occurrence of transients, trap response behaviour or any other biological reason. The quotients of residual deviance and residual degrees of freedom were not large for these data sets. Therefore, we concluded that the lack of fit was due to overdispersion of the data and retained the starting model for model selection. For five data sets with only one study year or only non-moulting birds available, we tested a starting model with correspondingly fewer parameters (Table 3) and consequently fewer models (Table 4).

Moult had a strong influence on stopover duration at most sites (Table 4), except at the most northern site (Rauvola) with few non-moulting reed warblers (21%), and at the two southernmost sites with only non-moulting reed warblers. Moulting reed warblers stayed far longer than non-moulting conspecifics (Fig. 2, Appendix 1). Out of eight sites with more than one study year available, only Mettnau showed a significant year effect (Table 4).

Average total stopover duration of non-moulting reed warblers was 9.5 ± 2.2 days (average of the mean values of all 12 sites \pm SD) and did not vary with latitude (linear regression of stopover duration of non-moulting reed warblers on latitude in year 1995: $F_{1,10}=1.02$, $P=0.34$; in 1996: $F_{1,9}=1.23$, $P=0.30$; Fig. 2).

Stopover duration of sedge warblers

Goodness-of-fit tests were significant for the data from two sites (Table 3), but no biological explanation was indicated by the subtests; hence, as in the reed warbler, the reason for the lack of fit was likely to be overdispersion

Table 3 Summary of tests of goodness of fit to the model $\{\phi_{m^*y^*t}, P_{m^*y^*t}\}$ for reed warblers and to the model $\{\phi_{y^*t}, P_{y^*t}\}$ for sedge and garden warblers, calculated with rel-cr. For some sites, some years are excluded, because they contributed to a significant goodness-of-fit test result (see text). The variance inflation factor \hat{c} was calculated as χ^2/df and is indicated only if the data were overdispersed; n is sample size. If the original starting model could not be used, an alternative model for which goodness-of-fit was tested is given

Species/Site	χ^2	df	P	\hat{c}	n	Alternative model
Reed warbler						
Rauvola	46.1	62	0.93	–	1,626	–
Lista ^a	37.5	38	0.49	–	952	–
Rybachy	150.1	121	0.04	1.241	1,592	–
Galenbecker See	113.6	89	0.04	1.277	1,724	–
Reit	54.6	47	0.21	–	511	$\{\phi_{m^*t}, P_{m^*t}\}$
Mettnau	78.5	67	0.16	–	2,176	–
Portalban ^b	76.1	70	0.29	–	1,012	–
Grône	47.0	37	0.13	–	399	$\{\phi_{m^*t}, P_{m^*t}\}$
Bolle di Magadino	103.7	84	0.07	1.234	1,020	–
Ebro Delta	92.9	55	<0.01	1.689	1,031	$\{\phi_{m^*t}, P_{m^*t}\}$
Coto de Doñana	13.2	11	0.28	–	90	$\{\phi_t, P_t\}$
Oued Moulouya	29.7	22	0.13	–	294	$\{\phi_{y^*t}, P_{y^*t}\}$
Sedge warbler						
Rauvola	55.5	60	0.64	–	2,554	–
Lista	65.1	77	0.83	–	1,405	–
Rybachy	74.5	29	<0.01	2.570	1,700	–
Galenbecker See	4.1	3	0.25	–	168	–
Illmitz	63.5	57	0.26	–	11,190	–
Bolle di Magadino	21.0	11	0.03	1.907	117	–
Garden warbler						
Rauvola	1.3	3	0.72	–	127	–
Rybachy	12.9	13	0.45	–	549	$\{\phi_t, P_t\}$
Greifswalder Oie	17.4	13	0.18	–	625	–
Helgoland	0.4	3	0.94	–	255	–
Oldeoog	28.6	16	0.03	1.786	918	–
Galenbecker See	1.7	2	0.42	–	164	–
Mettnau	14.7	13	0.33	–	490	–
Portalban	0.4	5	0.99	–	228	–
Coto de Doñana	16.8	10	0.08	1.684	1,678	–
Ginak	4.5	7	0.72	–	173	–

^a Only years 1994 and 1996 included

^b Only years 1987 and 1989 included

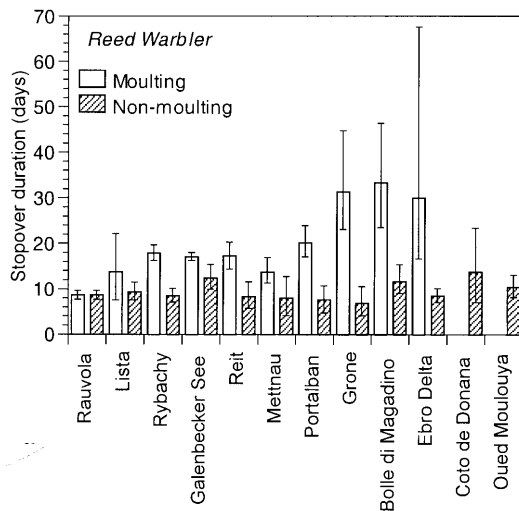


Fig. 2 Average total stopover duration and 95% confidence interval of non-moulting and moulting reed warblers at various sites (ordered from north to south), calculated with the most parsimonious models given in Table 4. For Mettnau and Ebro Delta the values for 1995 are shown

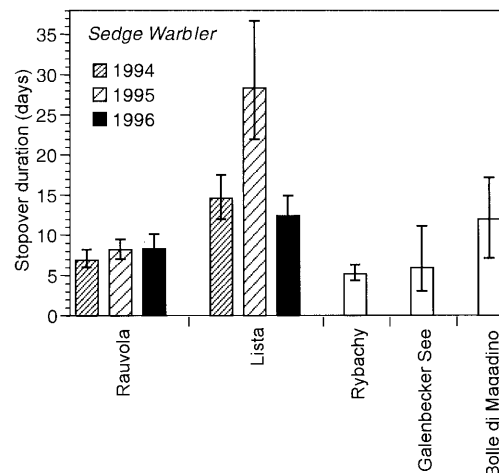


Fig. 3 Average total stopover duration and 95% confidence interval of sedge warblers at various sites (ordered from north to south) for each study year, calculated with the most parsimonious models given in Table 5. *Open bars* refer to the average of the three study years

of the data. At half of the sites, stopover duration differed between the study years (Table 5). The maximum difference in average stopover duration between years was small in Rauvola and large in Lista (Fig. 3, Appendix 1). At Illmitz, with 15 study years, average durations

differed considerably among years (Fig. 4) with a maximum difference of 7 days. The data sets of the sites without a year effect were either small (Galenbecker See and Bolle di Magadino) or overdispersed (Rybachy). Both tend to a selection of models with fewer parameters. In-

Table 4 Results of the model selection for stopover duration of reed warblers before and after capture among the candidate models. The values given are the differences $\Delta_i = \text{QAICc}_i - \text{QAICc}_{\min}$

Site	$\gamma_{m^*y}/\phi_{m^*y}, P_{m^*y^*t}$		$\gamma_{m^*y}/\phi_{m^*y}, P_{m^*y}$		$\gamma_m/\phi_m, P_{m^*t}$		$\gamma_m/\phi_m, P_m$		$\gamma_y/\phi_y, P_{y^*t}$		$\gamma_y/\phi_y, P_y$		$\gamma/\phi, P_t$		$\gamma/\phi, P$	
	γ	ϕ	γ	ϕ	γ	ϕ	γ	ϕ	γ	ϕ	γ	ϕ	γ	ϕ	γ	ϕ
	Rauvola	13.0	44.3	12.7	22.0	9.7	13.7	6.1	12.9	10.8	16.0	8.8	15.4	0.0	0.0	1.8
Lista	32.0	59.3	5.3	5.2	14.5	24.2	0.0	0.0	21.7	7.5	5.8	3.4	11.5	14.6	3.2	1.0
Rybachy	56.7	51.8	8.8	2.3	0.0	0.0	10.0	3.8	150.5	64.6	172.7	108.1	155.8	61.5	182.8	112.2
Galenbecker See	30.4	22.4	3.0	14.8	17.2	9.7	0.0	0.0	38.8	2.4	23.9	28.5	35.7	2.3	25.4	14.8
Reit	–	–	–	–	6.2	12.7	0.0	0.0	–	–	–	–	25.4	5.8	32.1	14.2
Mettnau	29.2	9.9	0.0	0.0	18.3	6.2	10.2	7.7	39.7	27.2	42.3	28.9	39.1	13.6	45.8	29.8
Portalban	57.9	47.7	2.1	4.2	25.0	18.0	0.0	0.0	90.9	31.5	65.3	32.6	74.5	22.5	67.2	30.5
Gröne	–	–	–	–	0.0	12.5	20.6	0.0	–	–	–	–	17.5	11.4	20.6	10.8
Bolle di Magadino	43.5	77.0	11.7	8.5	0.0	22.5	3.9	0.0	46.0	27.2	50.5	24.3	39.0	27.4	51.7	19.5
Ebro Delta	–	–	–	–	0.0	8.0	4.7	0.0	–	–	–	–	18.6	8.9	37.2	16.1
Coto de Doñana	–	–	–	–	–	–	–	–	–	–	–	–	18.2	9.4	0.0	0.0
Oued Moulouya	–	–	–	–	–	–	–	–	27.7	24.1	21.6	3.8	0.0	10.5	17.8	0.0

(QAICc modified Akaike information criterion). The most parsimonious models with $\Delta_i=0$, indicated in *bold*, were used for inferences

Table 5 Results of the model selection for stopover duration of sedge and garden warblers before and after capture among the candidate models. The values given Table are the differences

$\Delta_i = \text{QAICc}_i - \text{QAICc}_{\min}$. The most parsimonious models with $\Delta_i=0$, indicated in *bold*, were used for inferences

Site	$\gamma_y/\phi_y, P_{y^*t}$		$\gamma_y/\phi_y, P_y$		$\gamma/\phi, P_t$		$\gamma/\phi, P$	
	γ	ϕ	γ	ϕ	γ	ϕ	γ	ϕ
Sedge warbler								
Rauvola	0.0	14.3	23.4	0.0	2.4	8.3	25.6	1.0
Lista	0.0	0.0	14.1	53.1	115.3	140.5	100.3	152.7
Rybachy	36.1	36.8	4.5	5.1	6.0	10.9	0.0	0.0
Galenbecker See	129.0	132.4	1.5	1.9	13.0	17.8	0.0	0.0
Illmitz	54.2	91.7	0.0	0.0	24.2	4.1	29.6	26.7
Bolle di Magadino	93.9	90.2	6.8	6.2	20.1	19.5	0.0	0.0
Garden warbler								
Rauvola	32.6	43.2	7.7	7.3	0.0	8.3	1.2	0.0
Rybachy	–	–	–	–	9.7	0.0	0.0	2.7
Greifswalder Oie	0.0	8.7	16.5	0.0	9.7	9.2	20.0	2.8
Helgoland	22.6	26.1	2.0	2.1	0.2	5.6	0.0	0.0
Oldeog	35.1	52.9	3.9	4.0	5.5	13.4	0.0	0.0
Galenbecker See	31.7	35.5	2.8	2.1	8.4	5.5	0.0	0.0
Mettnau	23.5	38.3	1.7	1.3	12.7	5.6	0.0	0.0
Portalban	57.2	48.7	5.4	5.1	12.1	11.0	0.0	0.0
Coto de Doñana	44.4	47.2	4.5	4.6	13.1	10.7	0.0	0.0
Ginak	22.6	15.7	3.6	3.2	2.2	5.6	0.0	0.0

deed, the difference in QAICc between models with and without year effects was small for these three sites, indicating that the model selection uncertainty was considerable (Table 5).

Total stopover duration did not change with latitude in any year (Illmitz excluded because situated on the eastern migration route; 1994: $F_{1,3}=0.11$, $P=0.76$; 1995: $F_{1,3}=0.10$, $P=0.77$; 1996: $F_{1,3}=0.16$, $P=0.72$; Fig. 3). Average total stopover duration was 9.1 ± 5.2 days (average of the mean values of all 6 sites), hence slightly lower, but more variable, than those of non-moulting reed warblers (Figs. 2, 3, 4). At three out of five sites

where the two species occurred together, stopover duration of sedge warblers was lower than that of reed warblers.

Stopover duration of garden warblers

Goodness-of-fit tests were significant for datasets from two out of ten sites. The significant test result ($\chi^2_{41}=62.6$, $P<0.05$) in Rybachy was caused by a significant proportion of transients in the years 1995 and 1996, and we therefore only considered data from 1994. We

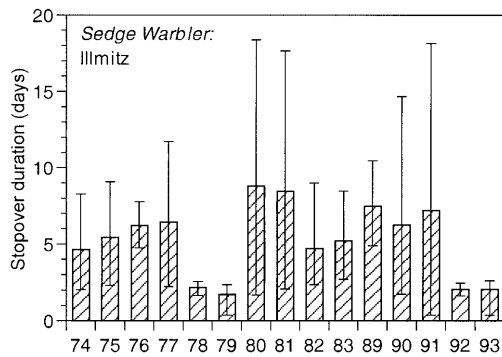


Fig. 4 Average total stopover duration and 95% confidence interval of sedge warblers at Illmitz for each study year, calculated with the most parsimonious model given in Table 5

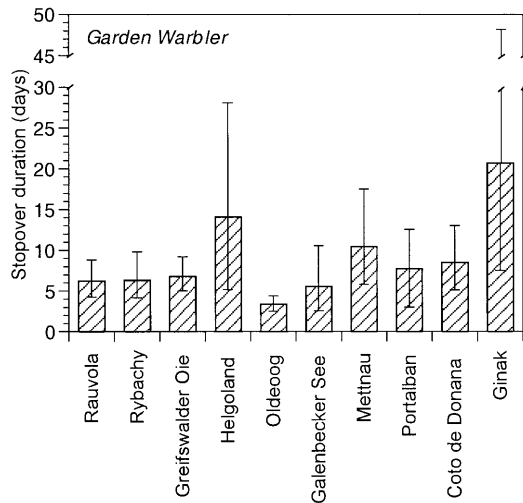


Fig. 5 Average total stopover duration and 95% confidence interval of garden warblers at various sites (ordered from north to south), calculated with the most parsimonious models given in Table 5

could not find biological reasons for the lack of fit of the data from Oldeog and supposed that it was caused by overdispersion of the data (Table 3). There was no significant effect of year, except at Greifswalder Oie (Table 5). For this site, model selection favoured models with different survival and recruitment parameters in the two study years; in 1995 the estimated stopover time before capture was longer than in 1996 and in 1996 the estimated stopover time after capture was longer than in 1995, so that total stopover duration differed only slightly between the two years (Appendix 1).

Mean stopover duration of garden warblers in Europe was 7.7 ± 3.1 days (average of the mean values of all 9 sites, except Ginak) and tended to be, though not statistically significantly, shorter than those of non-moulting reed and sedge warblers. Average total stopover duration did not vary with latitude within Europe (linear regression with latitude, 1995: $F_{1,7}=0.47$, $P=0.52$; 1996: $F_{1,7}=0.50$, $P=0.50$; Fig. 5). At Ginak (Gambia), which is situated south of the Sahara, garden warblers stayed longer than at stopover sites in Europe,

and probably continued southwards migration from there much slower.

Discussion

Method

As shown for other data sets, stopover durations estimated with the newly developed method (Schaub et al. 2001) used in this study were considerably longer than those estimated by previous methods. Indeed, average stopover duration derived from the ad hoc method (minimum stopover period) is only 6.4 days for the garden warbler and 5.7 days for the reed warbler at Mettnau in the years 1972–1989 (Kaiser 1996), compared to 10.5 days for garden warbler and 6.8–17.7 days (depending on year and moult status) for the reed warbler found in this study. However, stopover duration estimated with our approach is still underestimated, because birds that die during stopover are treated as having left the site. The bias is between 5 and 10% for a 10-day stopover duration assuming that the annual survival rate is 0.3–0.4 and constant over the year.

For the purpose of comparing sites and species, we estimated a single value of average stopover duration for a given site by controlling only for a restricted number of variables which are likely to have a large effect on stopover duration. A set of candidate models was defined a priori, which allows powerful inferences (Burnham and Anderson 1998). However, it is possible that models including additional variables will reveal further factors influencing stopover duration, and that stopover durations are not constant over the season.

Influence of moult

Moulting reed warblers stayed considerably longer at a site than non-moulting conspecifics. This may have two reasons. First, feather replacement requires energy which cannot be allocated to fuel deposition and, consequently, fuel deposition rates of moulting birds are lower (Schaub and Jenni 2000a). Therefore, moulting reed warblers would require more time to accumulate enough fuel for the next flight bout, and migration speed is low. In southern Europe, moult in reed warblers is generally completed which allows a higher fuel deposition rate and shorter stopovers, resulting in increased migration speed.

The second reason that might explain a longer stopover duration of moulting reed warblers is that it is difficult to separate locally born birds from birds already on migration. While it has been shown that reed warblers migrate across Europe while still moulting (Herremans 1990; Schaub and Jenni 2000a), the degree of overlap of moult and migration remains unknown. Hence, the samples probably include an unknown pro-

portion of locally born birds not yet on migration, although we restricted the study period to the main migration season at each site (Table 1). This explanation is supported by the finding that moulting reed warblers stayed longer at a site before capture than thereafter (Appendix 1).

Differences between years

Average stopover duration of garden warblers differed between years at only one out of nine sites and in reed warblers at one out of eight sites. For the sedge warbler, clear differences in average stopover duration between years were found at Lista and Illmitz. At Illmitz, average stopover duration was usually between 5 and 9 days, except for 1978, 1979, 1992 and 1993 with much shorter stopover durations (Fig. 4). For the remaining four sites, the uncertainty in selection ($\Delta_i < 7$) of models with and without years effects was considerable (Table 5). Therefore, it may be that the variation in stopover duration between years is more pronounced in the sedge warbler than in the reed and the garden warbler, as might be expected because of the higher annual variation in prey abundance for sedge warblers.

Differences between species

Stopover duration, averaged over all sites, was longest in reed warblers (9.5 days), intermediate in sedge warblers (9.1 days) and shortest in garden warblers (7.7 days). This pattern correlates negatively with average fuel deposition rates, as derived from birds re-trapped at these sites (Schaub and Jenni 2000a): rates were lowest in reed warblers, intermediate in sedge warblers and highest in garden warblers. If we assume that the birds have flight bouts of 450 km (ground speed 45 km h⁻¹, 10 h flight during a night; Bruderer 1997) over continental Europe, average speed of migration including the stopover times given above would be 47.4 km day⁻¹ for reed warblers, 49.5 km day⁻¹ for sedge warblers and 58.4 km day⁻¹ for garden warblers. This agrees with the overall migration speed as calculated from recoveries of birds ringed in northern Europe which was lowest in reed warblers (39–56 km day⁻¹; Hildén and Saurola 1982; Ellegren 1993; Bensch and Nielsen 1999), intermediate in sedge warblers (45–89 km day⁻¹; Hildén and Saurola 1982; Ellegren 1993; Bensch and Nielsen 1999) and highest in garden warblers (53–102 km day⁻¹; Hildén and Saurola 1982; Ellegren 1993; Fransson 1995).

Increasing speed of migration towards south?

In contrast to these differences between species, stopover duration within species did not vary very much between

sites and, within the data available, there was no systematic change of stopover duration with latitude (Figs. 2, 3, 4, 5).

The analysis of recoveries indicates that the speed of migration increases towards the south (Ellegren 1993), although this may be due to methodological effects (Bensch and Nielsen 1999). As we did not find a decrease in stopover duration towards the south, a possible increase in migration speed along the migration route is probably due to an increase in the length of flight bouts, which either requires a concomitant increase in fuel stores at departure or an increasing probability of encountering favourable winds. In reed warblers, an increase in fuel deposition rate towards the south was found (Schaub and Jenni 2000a) resulting in higher fuel stores at departure. In garden warblers, energy stores increase towards the south, but fuel deposition rates do not (Schaub and Jenni 2000a, 2000b). Hence, garden warblers apparently do not use all the energy accumulated at a stopover site for the following flight bout. Data on fuel deposition rates in southern Europe are not available for the sedge warbler (see next section for the organisation of migration of this species). Hence, reed and garden warblers increase the fuel stores available for the oncoming flight bout along the migration route and may increase the distance covered by a flight bout. At least in northern and central Europe, night migrants often fly only during the first part of the night (Ellegren 1993; Bruderer 1997). Increasing fuel loads may, therefore, enable birds to fly longer during a night or to fly during two consecutive nights across Europe. The meteorological conditions in central Europe are characterised by rapid passages of cyclones and prevailing westerly winds, whereas the conditions in southern Europe are less variable and the wind directions more favourable for birds migrating in a south-westerly direction (Liechti and Bruderer 1998). Thus, in southern Europe flight speed might be higher and the distance covered during a night larger. Hence, it remains to be discovered whether the increasing migration speed is due to a change in the behaviour of the bird by varying the length of flight bouts or whether this happens passively due to the more favourable winds in southern Europe.

Migration organisation

From the findings presented here, from the analysis of data on moult, fuel deposition rate and body mass collected within the same project (Schaub and Jenni 2000a, 2000b), and from literature data on moult, habitat and food, the organisation of autumn migration of the three species can be characterised as follows.

In northern and central Europe, reed warblers feed on a rather evenly distributed, predictable food resource, occurring generally at low density and declining with season (Bibby and Green 1981; Turrian and Jenni 1991). It appears best for reed warblers to leave

northern sites as early as possible, i.e. when still moulting (Herremans 1990). This, however, prevents extensive fuel deposition (Schaub and Jenni 2000a). Stopover duration is long at this stage (this study) and overall migration speed low (see previous sections). When moult is completed (in southern Europe at the latest; Schaub and Jenni 2000b), fuel deposition rate increases (Schaub and Jenni 2000a), stopover duration decreases (this study) and migration speed increases (see previous section). Body masses including energy stores remain constant along the migration route in Europe (Schaub and Jenni 2000b). The energy needed to cross the Sahara is accumulated just before it, apparently by faster fuel deposition and not by longer stopover. This may be attained by extending the types of habitats used, and would explain why reed warblers in the Mediterranean region commonly feed in habitats other than reedbeds (Glutz von Blotzheim and Bauer 1991; authors, personal observations).

Sedge warblers rely on reed aphids which are clumped and often superabundant. Superabundance of reed aphids is unpredictable in space and between years (Hanski and Woiwod 1993), but enables sedge warblers to fuel up very quickly when peaks occur. Reed aphid abundance in southern Europe peaks before the onset of migration (Bibby and Green 1981) and hence the birds should not rely on stopover sites in the south. The best strategy for sedge warblers appears to be to start migration as early as possible (before moult, Redfern and Alker 1996) and, as soon as they encounter a site with superabundant food anywhere in Europe, to fuel up extensively and to fly without much further refuelling directly to sites south of the Sahara where they moult (Bibby and Green 1981; Redfern and Alker 1996; Schaub and Jenni 2000a). Moult before autumn migration is probably incompatible with unpredictable extensive fuelling. Hence, fuel deposition rates and stopover durations are variable between sites and years (Schaub and Jenni 2000a; this study).

Garden warblers switch from an entirely invertebrate diet during the breeding season to a mixed diet containing a large proportion of fruit during their autumn migration (Simons and Bairlein 1990). Thus, they harvest a predictable, rich and long-lasting food supply which allows fast fuel deposition (Schaub and Jenni 2000a). Consequently, garden warblers can conveniently moult prior to migration (Berthold et al. 1972), stopover duration is generally short (this study) and migration speed high (see previous sections). Body mass increases towards south and they are thus less dependent on good stopover sites (high fuel deposition rates) or long stopovers just north of the Sahara than the reed warblers (Schaub and Jenni 2000b).

Perspectives

A surprising finding of this study is that stopover duration is quite similar across sites along the migration

route (especially conspicuous in non-moulting reed warblers). It is unknown how stopover duration is regulated, and the following hypotheses have been proposed. Firstly, there might be an innate rhythm of flight and refuelling periods which provide the frame of stopover duration. Rhythmic body mass changes of about 2 weeks in garden warblers kept under standard conditions during the migratory season may hint at such a phenomenon (Bairlein 1986). This fits well with the rather constant stopover durations between sites found in our study. Secondly, the decision to depart might be determined by the actual fuel stores or by the fuel deposition rate. Theoretical models predict that the departure fuel load should increase with fuel deposition rate if the birds are selected to save time spent on migration (Alestrom and Lindström 1990; Weber and Houston 1997). Thirdly, stopover duration might be determined by wind conditions aloft. Birds can gain much potential flight range by selecting nights with favourable winds (Liechti and Bruderer 1998; Weber et al. 1998a). A theoretical model shows that the decision to depart should depend on the probability and the amount of wind assistance (Weber et al. 1998a). Fourthly, stopover duration might be dependent on predation risk. Blackcaps (*Sylvia atricapilla*) exposed to predator dummies had a higher tendency to leave a site than unexposed birds (Fransson and Weber 1997).

Most of these hypotheses have so far not been tested empirically. Reliable estimation of stopover duration, as proposed by Schaub et al. (2001) and applied in this study, and the analysis of field data on different bird groups will allow testing of some of the proposals on how stopover duration is regulated. For example, empirical data can be used to test whether wind conditions aloft influence stopover duration and departure in the way predicted by the theoretical models, or whether birds depart with similar fuel stores, which would help understanding of the relationship between stopover duration and fuel stores.

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Appendix

Reed warbler

Table A1. Average stopover durations (95% confidence interval in parentheses) before and after capture estimated with the most parsimonious models given in Tables 4, 5. For sites with a year effect, estimates for the different years are given separately. From the figures in this table, average total stopover duration (and its 95% confidence interval) can be calculated by adding the figures given for stopover duration (and 95% confidence intervals, respectively) before and after capture (see Figs. 2, 3, 4, 5)

Site/Year	Non moulting		Moulting	
	Before	After	Before	After
Rauvola	4.4 (3.9–4.9)	4.3 (3.8–4.7)	4.4 (3.9–4.9)	4.3 (3.8–4.7)
Lista	4.7 (3.8–5.8)	4.6 (3.7–5.6)	7.5 (4.0–12.8)	6.3 (3.6–9.3)
Rybachy	4.0 (3.4–4.8)	4.5 (3.6–5.5)	9.4 (8.5–10.3)	8.5 (7.7–9.4)
Galenbecker See	6.4 (5.1–8.1)	6.1 (4.9–7.4)	9.4 (8.9–10.1)	7.6 (7.2–8.1)
Reit	4.3 (2.9–6.0)	4.1 (2.8–5.7)	9.8 (8.0–11.7)	7.5 (6.4–8.6)
Mettnau 1995	4.1 (2.1–6.7)	3.9 (2.1–6.1)	7.6 (6.1–9.5)	6.2 (5.2–7.4)
Mettnau 1996	3.7 (2.5–5.0)	3.1 (2.2–4.2)	9.9 (6.1–15.5)	7.8 (5.3–10.7)
Portalban	3.9 (2.3–5.3)	3.8 (2.3–5.3)	12.4 (10.2–15.1)	7.9 (7.0–8.8)
Gröne	3.7 (2.5–5.2)	3.1 (1.5–5.7)	21.4 (14.5–33.4)	9.9 (8.4–11.5)
Bolle di Magadino	6.1 (4.7–8.1)	5.7 (4.3–7.3)	22.7 (14.8–34.2)	10.5 (8.7–12.5)
Ebro Delta	4.9 (3.8–6.1)	3.6 (3.2–4.1)	23.6 (11.1–60.1)	6.4 (5.3–7.5)
Coto de Doñana	7.7 (3.9–13.2)	6.2 (3.3–9.5)	–	–
Oued Moulouya	5.8 (4.3–7.7)	4.7 (3.8–5.4)	–	–

Sedge warbler

Table A2. Average stopover durations (95% confidence interval in parentheses) before and after capture estimated with the most parsimonious models given in Tables 4, 5. Details as in Table A1

Site	Before	After
Rauvola 1994	3.6 (3.0–4.2)	3.3 (2.8–4.0)
Rauvola 1995	4.5 (3.9–5.2)	3.7 (3.1–4.3)
Rauvola 1996	4.5 (3.6–5.5)	3.8 (3.1–4.6)
Lista 1994	8.9 (7.1–11.2)	5.7 (5.0–6.3)
Lista 1995	15.9 (11.3–22.3)	12.4 (10.0–15.7)
Lista 1996	6.2 (4.9–7.2)	6.2 (5.2–7.7)
Rybachy	2.6 (2.1–3.1)	2.6 (2.1–3.2)
Galenbecker See	3.0 (1.5–5.6)	2.9 (1.5–5.5)
Illmitz 1974	2.4 (1.0–4.4)	2.2 (1.0–3.8)
Illmitz 1975	3.0 (1.2–5.2)	2.5 (1.1–3.9)
Illmitz 1976	3.4 (2.5–4.3)	2.8 (2.2–3.4)
Illmitz 1977	3.5 (1.1–6.7)	3.0 (1.1–5.2)
Illmitz 1978	1.1 (0.8–1.3)	1.1 (0.8–1.2)
Illmitz 1979	0.9 (0.2–1.2)	0.9 (0.2–1.1)
Illmitz 1980	4.8 (0.8–10.6)	4.0 (0.8–7.8)
Illmitz 1981	4.5 (1.1–9.8)	3.9 (1.0–7.9)
Illmitz 1982	2.4 (1.2–4.7)	2.3 (1.2–4.3)
Illmitz 1983	2.8 (1.4–4.7)	2.4 (1.3–3.8)
Illmitz 1989	4.1 (2.6–5.9)	3.4 (2.3–4.6)
Illmitz 1990	3.2 (0.9–7.7)	3.0 (0.9–6.9)
Illmitz 1991	3.9 (0.2–10.4)	3.3 (0.2–7.8)
Illmitz 1992	1.1 (0.8–1.3)	1.0 (0.8–1.2)
Illmitz 1993	1.0 (0.2–1.3)	1.0 (0.2–1.3)
Bolle di Magadino	5.7 (3.5–7.8)	6.3 (3.6–9.4)

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Garden warbler

Table A3. Average stopover durations (95% confidence interval in parentheses) before and after capture estimated with the most parsimonious models given in Tables 4, 5. Details as in Table A1

Site	Before	After
Rauvola	3.3 (2.4–4.8)	2.9 (1.8–4.5)
Rybachy	3.2 (2.2–5.1)	3.1 (2.0–4.8)
Greifswalder Oie 1995	5.0 (1.9–12.4)	2.4 (1.2–4.0)
Greifswalder Oie 1996	4.2 (3.0–6.0)	2.6 (1.8–3.5)
Helgoland	7.0 (2.6–14.1)	7.1 (2.6–14.0)
Oldeog	1.7 (1.2–2.2)	1.7 (1.2–2.2)
Galenbecker See	2.9 (1.3–5.5)	2.7 (1.2–5.0)
Mettnau	5.5 (3.0–9.5)	5.0 (2.9–8.0)
Portalban	4.0 (1.5–6.5)	3.8 (1.5–6.0)
Coto de Doñana	4.4 (2.6–6.8)	4.1 (2.5–6.2)
Ginak	13.7 (3.8–37.5)	7.0 (3.2–10.3)

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