

Variation in the stopover duration of Reed Warblers *Acrocephalus scirpaceus* in Morocco: effects of season, age and site

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To test the prediction that stopover duration reflects the rate of body mass gain during stopover, the relationship between these two parameters was investigated in the Reed Warbler *Acrocephalus scirpaceus* at two sites in Morocco, Sidi Bou Ghaba on the Atlantic coast, and Kerbacha on the Mediterranean coast. Estimation of stopover duration was made using the recently published method by M. Schaub *et al.* We investigated effects of age and site on stopover parameters during autumn and spring migration. Stopover duration was longer for juveniles than for adults, longer at the Atlantic site than at the Mediterranean site and longer in autumn than in spring. Altogether, estimated stopover duration was longer than expected from previous studies based on minimum stopover duration. Body mass gain varied inconsistently among site, season and age classes, without a clear relation to stopover duration. This suggests that stopover duration is not dependent only on the rate of body mass gain.

Migrating birds usually have to divide their migration route into several flights separated by stopovers (Bairlein 1985, Biebach *et al.* 1986). During these stopovers, individuals must restore their energy reserves. The energy thus gained will be used during the following flight (Berthold 1975, 2001, Blem 1980, Bairlein 2002). The alternation of stopovers and flights, as well as body mass gains during stops, defines the migration strategy of the species considered (Alerstam & Lindström 1990, Alerstam & Hedenström 1998). These strategies can differ between species, between populations of the same species (Ellegren 1991), and between age and sex classes within the same population (Ellegren 1990). Overall, predictive models of migration strategy assume a negative relationship between stopover duration and rate of energy gain (Bairlein 1985, Biebach 1985, Pettersson & Hasselquist 1985, Biebach *et al.* 1986, Alerstam & Lindström 1990, Berthold & Terrill 1991, Yong & Moore 1997).

Determining the migration strategy of a given group and comparing strategies between groups requires

stopover duration to be estimated. For passerines, this is typically achieved through the capture, ringing and recapture of individuals at stopover sites. The minimum stopover duration (MSD) has been estimated as the time elapsed between first and last capture of a given individual (Cherry 1982, Lyons & Haig 1995, Moris *et al.* 1996, Yong *et al.* 1998). MSD is clearly related to the actual stopover duration. However, the amount of capture effort and the distribution of effort during the study period affect the relationship between minimum and actual stopover duration, making the reliability of the comparison of MSD between groups questionable. Recent developments in capture–mark–recapture (CMR) methodology allow the estimation of actual stopover duration, taking into account possible variation in the capture probability over time and among groups (Schaub *et al.* 2001). Such methods not only allow evaluation of actual stopover duration, but also straightforward comparisons among groups.

Here, we used this methodology to estimate stopover duration of the Reed Warbler *Acrocephalus scirpaceus* in Morocco. We analysed capture–recapture data collected at two sites, in several years during autumn

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and spring migrations (nine season–year–site combinations). This data set allowed us to study variation in stopover duration between seasons, age-classes and sites. Although all these factors are known to affect stopover duration, they are rarely studied simultaneously. Furthermore, the use of the method by Schaub *et al.* (2001) considerably improved the consistency of these comparisons. We combined this analysis with a study of the rate of body mass gain per day, again comparing variation between seasons, sites and age-classes. We predicted that if migration strategy is largely a matter of a trade-off between staying longer and refuelling sufficiently, there should be a negative relationship between stopover duration and mass gain speed among the different groups.

MATERIALS AND METHODS

Study site

Capture–recapture studies were conducted in two Moroccan wetlands: the ‘Réserve Biologique’ of Sidi Bou Ghaba (SBG in the following) and the riverside woodland of Kerbacha.

Sidi Bou Ghaba (34°13'N, 06°42'W) is one of the four Moroccan Ramsar sites; it is close to the Atlantic coast, 30 km north-east of Rabat. The site consists of a shallow lake of brackish water with dense vegetation along the shore (e.g. *Juncus maritimus*, *J. acutus*, *Typha angustifolia*, *Phragmites australis*, *Scirpus maritimus*, *Chenopodium chenopodioides*, *Populus alba*), and 450 ha of matorral woodland primarily of *Juniperus phoenicea*, *Retama monosperma* and *Olea europea* (Atbib 1979, Harrache 1994).

Kerbacha (35°04'N, 02°13'E) is located on the Mediterranean coast, near the western limit of the Oued Mansour hills, 8 km from Saidia. It is located on the eastern edge of the woody area Wad Moulaya. The vegetation is dominated by *Tamarix canariensis* along the rivers, in addition to *Arthrocnemum macrostachyum*, *Suaeda vera*, *Juncus rigidus*, *J. acutus*, *Scirpus maritimus*, *Scirpus lacustris* and *Phragmites australis* (Dakki *et al.* 2002).

Species

The Reed Warbler is a Palaearctic passerine and a widespread breeder from North Africa to Central Asia; it reaches its northern European limit in England and southern Fennoscandia (Cramp 1992).

In the northern winter, European Reed Warblers move to tropical Africa (Moreau 1972, Cramp 1992,

Urban *et al.* 1997). In Morocco, the distribution is governed by the presence of reed-beds (Géroutet 1980, Bairlein 1983). Reed Warblers are present in high numbers during spring and autumn migrations and are rare winter visitors (Rguibi-Idrissi 2002, Thévenot *et al.* in press). Fewer than 20 pairs breed at Sidi Bou Ghaba (Rguibi-Idrissi *et al.* 2002), but breeding individuals were easily recognized by prominent sexual characteristics (brood patch in females, development of the cloacal protuberance in males) and wing length and excluded from the analysis.

Data set

At a given site, year and season, a set of mist-nets was open daily from dawn to sunset, except during periods of high precipitation or violent wind (less than 5% of the days). The number of mist-nets varied between site, year and season, but remained constant for a given season, year and site. Nets were concentrated in a limited area where capture effort was thus maximized. Birds were individually ringed (Helgoland rings, Wilhelmshaven, Germany) and weighed to the nearest 0.1 g with a Salter spring balance (60 g). Most individuals were aged, separating birds in their first year from older ones on plumage, eyes and/or tongue coloration (Svensson 1992, Jenni & Winkler 1994).

All days between the first and last date of recorded capture in a given site, year and season were considered as potential days of capture (whether any birds were captured or not; Table 1), and the capture–recapture history of each individual was constructed on this basis.

Statistical analysis

Stopover duration

Estimation of stopover duration was made using the recent method developed by Schaub *et al.* (2001), using the software SODA (Schaub *et al.* 2001). Minimum stopover duration is calculated as the number of days elapsed between first and last capture for a given individual. However, not all individuals present on a given day are captured. Hence, a given individual may have arrived in the study site some days before its first capture and may have left the study site some days after its last capture. The sequence of captures and recaptures of individuals caught during the study period can be analysed using classic CMR methodology. This allows the estimation of several

Table 1. Period of ringing and numbers of juvenile and adult Reed Warblers captured and recaptured during stopover at two sites in Morocco.

Season	Kerbacha (Mediterranean site)			Sidi Bou Ghaba (Atlantic site)		
	No. of captures (recaptures)			No. of captures (recaptures)		
	Trapping period	Juveniles	Adults	Trapping period	Juveniles	Adults
Aut. 1994	10/9–29/10	213 (39)	46 (9)	10/9–29/10	53 (13)	62 (7)
Aut. 1996	16/8–26/10	93 (39)	26 (5)			
Aut. 1999				19/8–20/10	64 (39)	25 (14)
Aut. 2000				1/9–26/10	108 (36)	101 (33)
Spr. 1994	15/4–15/5	56 (14)	345 (102)			
Spr. 1996	3/4–29/5	46 (9)	56 (3)			
Spr. 1999				27/3–7/6	49 (22)	25 (11)
Spr. 2000				30/3–31/5	162 (31)	288 (32)

parameters: (1) capture probability on a given occasion (i.e. day); (2) local survival probability from the day of first capture (Lebreton *et al.* 1992), which is one minus the emigration probability – from this we can estimate the duration of stay from the day of first capture (as can life expectancy be calculated from survival probability); (3) local seniority probability (proportion of the population that was already there at the previous capture occasion; Pradel 1996) which is one minus the immigration probability – from this can be estimated the duration of stay before the day of last capture. Hence, for a given day of capture, the expected number of days before departure and the expected number of days since arrival of individuals present in the study site can be estimated. The sum of both is an estimation of the expected stopover duration of individuals present on that day.

Because we were interested in the comparison of stopover duration among groups, we chose a model giving an average estimate of stopover duration for a given age-class, season, year and site, and we used the same model for all estimations. Because of the large number of capture occasions we could neither use complicated models nor assess the models by the use of goodness-of-fit tests. In particular, models allowing for heterogeneity of capture probability did not converge for several data subsets. We chose a model allowing capture probability to vary with time while keeping the two other parameters constant (models [ϕ , $p(t)$] and [γ , $p(t)$] in the denomination of SODA). We used the original method of interpolation (see Schaub *et al.* 2001), which is the only one giving a constant estimation of stopover duration with the model chosen.

In a second step, we analysed stopover duration estimates in a weighted analysis of variance with site, season and age as control variables. Estimates are usually weighted by the inverse of the squared standard error ($1/se^2$). However, because the variable estimated is a duration (a positive number), the standard error is typically proportional to the value of the estimate. Hence estimates were log-transformed before analysis, and weights used were $1/(cv^2)$.

Body mass variation

We studied individual body mass variation as a complementary characteristic of migration strategy. We modelled between- and within-individual body mass variation separately. We first analysed body mass at first capture for all individuals aged and weighed, and how it varies with season, age and site. We then studied changes of body mass for individuals captured several times within a season. We were interested in body mass change as a function of the number of days since first capture, and how this relation differed between sites, seasons and age-classes. Two variables were 'constructed': 'day', which is the number of days since the first capture of a given individual in a given season, taking the value 0 for first capture, and 'individual number', which is a qualitative variable characterizing an individual caught in a given season at a given site (when the same individual was captured and recaptured in different seasons, it was given different numbers in each season). The linearity of the relationship between body mass and day was assessed with non-parametric spline regression in a general additive model (GAM) implemented in SPLUS.

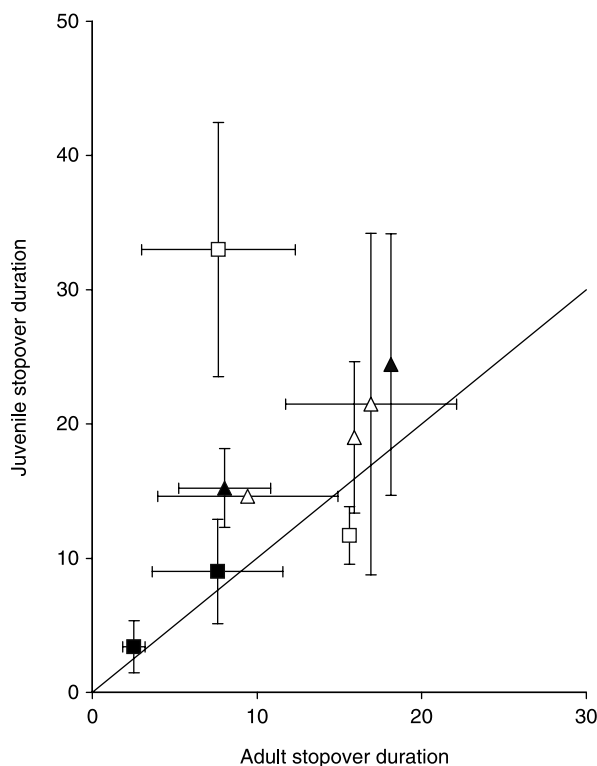


Figure 1. The relationship between estimated stopover duration of juvenile and adult Reed Warblers captured at a given site, year and season (\pm se; if se is greater than 15 days, error bars are omitted for clarity). Squares: Kerbacha; triangle: Sidi Bou Ghaba; open symbols: autumn; filled symbols: spring. The line indicates equal stopover duration of juveniles and adults at a given site, season and year.

RESULTS

Stopover duration of Reed Warblers

The average stopover duration was estimated independently for each season, site, year and age-class (18 estimations; Fig. 1). The effects of season, site and age were estimated in a weighted ANOVA (Table 2). All effects were statistically significant, with juveniles stopping longer than adults, stopover being longer during autumn than spring, and longer on the Atlantic site (Sidi Bou Ghaba) than on the Mediterranean site (Kerbacha) (Fig. 1). Interactions between age and the other effects were tested in weighted ANOVAs including a qualitative cohort effect (equivalent to pairwise comparison; Table 3). Both interactions were non-significant, indicating a consistent effect of age across seasons and sites, as can be seen in Figure 1. The cohort effect was highly significant, indicating a positive correlation between

Table 2. Weighted ANOVA of stopover duration estimates (log-transformed). Test ($F_{1,14}$) and estimates for a given effect are adjusted to other effect (type III error). Estimates and se were back-calculated in days and indicate the difference between modalities of the effect (e.g. juveniles stop 5.4 days more than adults). The actual estimate can be found in Figs 1 and 3.

Effect	Estimate (days)	se	Test	<i>P</i>
Age (juv. vs. ad.)	+5.4	1.7	10.70	0.006
Site (SBG. vs. Ker.)	+4.9	1.5	10.68	0.006
Season (Aut. vs. Spr.)	+4.3	1.4	8.97	0.01

Table 3. Weighted ANOVA of stopover duration estimates (log-transformed) with cohort effect included. Cohort is a qualitative variable characterizing a given season, site and year (nine cohorts).

Effect	Test	<i>P</i>
Cohort	$F_{8,8} = 14.92$	0.0005
Age	$F_{1,8} = 14.41$	0.005
Age \times Season	$F_{1,7} = 0.64$	0.5
Age \times Site	$F_{1,7} = 0.13$	0.7

estimates of stopover duration of juveniles and adults for a given season, site and year (Fig. 1).

Body mass variation during stopover

Between-individual variation

Body mass at first capture was taken for 1722 individuals. There was a considerable season effect on body mass, with individuals weighing on average 1.58 g (+14%) more in autumn than in spring (Table 4). Adults tended to be heavier than juveniles (main effect of age: +0.28 g for adults vs. first year) across sites and seasons, but a significant site \times age \times season interaction indicated a lack of consistency in this tendency.

Within-individual variation

In total, 261 individuals were recaptured 383 times (i.e. a total of 644 captures). The linearity of the relationship between body mass and number of days after first capture was tested with GAM modelling. No important non-linearity was detected (test for non-linear effect $F_{3,375} = 1.22$, $P = 0.3$; Fig. 2) beyond the very strong linear effect ($F_{1,378} = 49.05$, $P < 0.0001$). Hence, body mass was considered to vary linearly with the number of days after first capture. How body mass variation differed between sites, seasons and age-classes was tested incorporating interactions between these effects and the variable

Table 4. Modelling body mass variation. (a) Body mass variation at first capture for all individuals captured (1714 residual *df*). (b) Within-individual variation for individuals recaptured at least once. Variable 'Day' is the number of days since first capture and account for linear variation of body mass as a function of time. Interactions thus test for variation of the linear relationship between body mass and 'day' among groups (371 residual *df*). Tests are not adjusted (Type I error). See estimates in Fig. 3. Interactions: A – Age, D – Day, Si – Site, Se – Season.

(a) Between-individual variation				(b) Within-individual variation			
Effect	df	F	P	Effect	df	F	P
Age	1	9.68	0.002	Individual no.	260	6.99	< 0.0001
Season	1	346.5	< 0.0001	Day	1	53.94	< 0.0001
Site	1	0.02	0.9	D × A	1	2.88	0.09
A × Se	1	2.36	0.12	D × Se	1	1.07	0.3
A × Si	1	0.01	0.9	D × Si	1	0.83	0.4
Se × Si	1	0.28	0.6	D × A × Se	1	0.32	0.6
A × Se × Si	1	13.05	0.0003	D × A × Si	1	30.75	< 0.0001
				D × Se × Si	1	4.05	0.04
				D × A × Se × Si	1	5.20	0.02

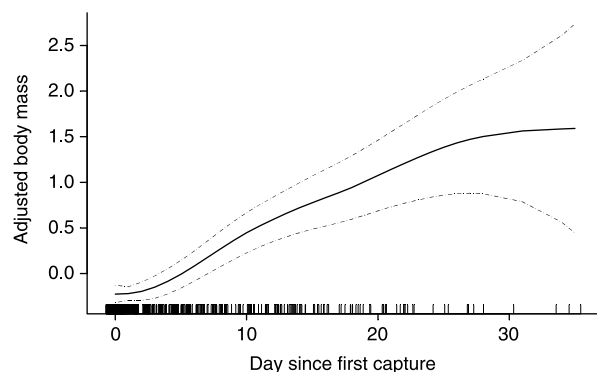


Figure 2. The relationship between body mass (g) and number of days after first capture of Reed Warblers recaptured at two stopover sites in Morocco (all data combined). Data were analysed with GAM modelling, adjusting weight among individuals (only within-individual weight variation was taken into account). Small vertical bars on the x-axis show the distribution of data. Broken lines are 95% confidence limits.

day (main effects were nested into individual effect and thus not estimable). The pattern of variation in body mass gain was rather complicated because the fourth-order interaction day × site × age × season was significant (Table 4). The slope between body mass and day after first capture was calculated for each group separately (Fig. 3).

DISCUSSION

Methodological considerations

For a given site, year and season (i.e. cohort), there was an excellent correlation between stopover

duration estimates for juveniles and adults (Fig. 1). Because estimations of capture probability, and immigration and emigration rates were made independently for each group, we do not see how this pattern could be due to a methodological artefact. Hence, we take this as evidence that the method is able to retrieve actual variation in stopover duration between groups.

As found by Schaub *et al.* (2001), the estimated stopover duration was considerably longer than previously thought from MSD estimates. Our estimates generally ranged between 10 and 20 days, whereas average MSD is typically around 3–4 days for this species (Lavee *et al.* 1991, Robson *et al.* 2001). Indeed, the geometric mean MSD calculated for our dataset was 3.7 (se = ±0.2) days.

Variation of migration strategy among groups

Using the recent method of Schaub *et al.* (2001), we confirmed the general assumption that stopover duration is longer in autumn than in spring and longer for first-year birds than for adults (Hedenström 1997, Restani 2000, Berthold 2001). We further showed that the age effect on stopover duration did not differ between two contrasting sites, and was the same in spring and in autumn. Individuals on their first spring migration stage for a longer time than more experienced individuals, despite having already experienced the autumn migration. Hence, either autumn migration does not serve as experience for the spring migration strategy or the age effect in spring is not due to lack of experience. Although

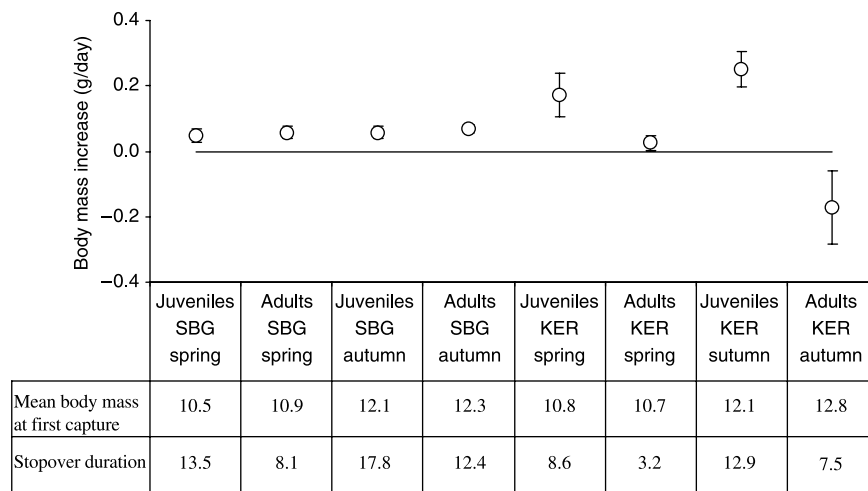


Figure 3. Rate of body mass gain (\pm se) of juvenile and adult Reed Warblers during spring and autumn stopover at two sites in Morocco (SBG = Sidi Bou Ghaba; KER = Kerbacha). Mean body mass (g) at first capture and estimated stopover duration (days) are shown.

there was no direct evidence before this study for a longer stopover duration for first-year birds than adults in spring, this is in accordance with the widespread observation in several migrating passerines that first-year birds arrive later on their breeding grounds than adults. For Reed Warblers, we show that a possible cause of this later arrival is a lower migration speed owing to longer stopovers.

The rate of body mass increase varied among sites, seasons and age-classes (Fig. 3). There were no effects of age or season at the Atlantic site with a very slow but significant daily body mass increase (average 0.058 g/day or 17 days required to increase body mass by 1 g) for all groups. At the Mediterranean site, however, first-year birds increased body mass rather rapidly (on average 0.21 g/day or less than 5 days required to increase body mass by 1 g), whereas the adults did not show a significant change in spring and even lost body mass during stopover in autumn. Surprisingly, variation in the within-individual rate of body mass gain appeared to be related inconsistently to variation in body mass at first capture. In particular, average body mass for a given age-class and season was rather similar at the two sites, whereas rate of body mass gain varied considerably between sites for a given age-class and season (Table 4 and Fig. 3).

According to conventional theory, individuals gaining body mass rapidly should have a shorter stopover than individuals gaining body mass slowly. However, this is not confirmed by the present results as there was no consistent relationship between

stopover duration and rate of fuelling among groups. Between-site comparisons in first-year birds fit the prediction, but this is true neither for within-site comparisons nor for between-site comparison of adults. It is likely that these differences reflect different migration strategies in autumn and spring, together with geographical influences. The longer stopovers during autumn reflect a less time-constrained southbound migration, whereas northbound in spring the birds are in a hurry to reach the breeding grounds as soon as possible (e.g. Cherry 1982, Veiga 1986, Izhaki & Maitav 1998, Young *et al.* 1998, Robson *et al.* 2001). During southbound migration these migrants are facing the Sahara, and thus they must fuel. This explains the higher rate of body mass gain in autumn in first-year birds at both sites, although less pronounced at the Atlantic site. There, the lower rate of mass gain may be due to a poorer food supply.

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