Stopover duration of Palearctic passerine migrants in the western Sahara – independent of fat stores?

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Birds on migration spend much more time on stopover sites to refuel for the next migration step than aloft, but empirical data on stopover duration are rare, especially for Palearctic trans-Sahara migrants whilst crossing the desert. Previous studies suggest that stopover duration of fat birds in oases is much shorter than that of lean birds. During 2003 and 2004 capture–recapture data of migrating passerines from two inland oases in spring and from one coastal site in autumn in Mauritania, West Africa, were analysed to test whether the probability of being a transient and the stopover duration depend on fuel stores at first capture. The application of capture–recapture models revealed that during autumn migration at the coast the proportion of transients (individuals that stop over only for 1 day) was relatively high (77–90%) in three out of four species investigated and stopover duration was short (1.9–4.6 days). In the inland oases in spring, transients were detected in only four out of 12 analyses. Stopover duration was longer than at the coast in autumn and surprisingly long in some species with durations of up to 30 days. Models taking into account the initial fat load of birds on the first capture occasion were, with one exception, never the most parsimonious ones. This indicates that the time spent after and before capture at the stopover site did not depend on the fat stores at first capture. Therefore, we cannot confirm the assumption that birds arriving at stopover sites in the desert with low fat loads stay longer than birds that arrive with high fat loads.

Birds from the Palearctic that winter in tropical Africa have to cross a vast ecological barrier, the Sahara Desert. Although we have relatively good knowledge regarding the migration strategies over Europe both on empirical (e.g. Bibby & Green 1980, Bensch & Nielsen 1999, Schaub & Jenni 2000a, 2000b, 2001, Dierschke *et al.* 2003) and on theoretical grounds (Alerstam & Hedenström 1998, Weber *et al.* 1998, Alerstam *et al.* 2003, Erni *et al.* 2003), relatively little is known about how birds manage to cross the Sahara (but see Biebach *et al.* 2000, Erni *et al.* 2003). Migrants allocate more time to stopover, where fuel for migration is restored, than to actual flight bouts (Lindström 1995). Although there are calculations of total migration speed (Alerstam & Lindström 1990, Ellegren 1993, Fransson 1995, Bensch & Nielsen 1999), time allocation of birds migrating across the desert is unknown. Mortality could be

substantial during migration (Ketterson & Nolan 1982, Sillett & Holmes 2002), and mortality is likely to be concentrated when a large inhospitable area with scarce refuelling possibilities and harsh environmental conditions has to be crossed. Therefore, investigations on the strategies adopted by migrants in crossing the Sahara are crucial for our understanding of individual life histories, of population dynamics and of the evolution of migration strategies.

Moreau (1961, 1972) suggested that passerines in the Palearctic–African migration system cross the Mediterranean Sea and the Sahara Desert in a 40–60-h non-stop flight on autumn migration. The non-stop theory was supported by observations that migrants do not concentrate in oases and that numbers of birds found in the desert during daytime were low compared with the estimated total number of migrants. Consequently, birds found in oases were assumed to be 'fall outs', not capable of further migration (Moreau 1961, 1972, Wood 1989). By contrast, Bairlein (1985, 1992) and Biebach *et al.*

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(1986) proposed an alternative intermittent strategy of desert crossing that involves regular stopovers in the desert. The main argument for the intermittent migration strategy was that a high proportion of migrant passerines found in the desert were in good physical condition (Bairlein *et al.* 1983, Bairlein 1985, 1992, Biebach 1995). The minimum stopover method (Borror 1948) was applied to estimate stopover duration in oases for birds with high and low initial fat loads. Fat birds were often captured only once, which suggested that they resume migration the night following arrival (Bairlein 1985, Biebach 1985, Biebach *et al.* 1986, Gannes 2002). By contrast, lean birds were often captured repeatedly, suggesting that they stopped over in oases for several days to replenish depleted fuel stores (Bairlein 1985, Biebach 1985, Biebach *et al.* 1986). Other possible factors that might influence departure decisions, such as distance of migration, weather, experience and season (Lavee & Safriel 1989, Loria & Moore 1990, Schaub *et al.* 2004), were not studied.

The view that most birds use an intermittent strategy, with fat birds making short stopovers in the desert without significant refuelling and with lean birds making longer stopovers and significant refuelling, relies on the assumption that the probability of catching birds at a stopover site is independent of fat stores and implies that fuel store is the only factor influencing departure decisions from stopover sites. However, the greater activity of lean birds (Bairlein 1985) may well result in higher recapture rates of lean birds than fat birds. This problem can be overcome by the application of capture–recapture models, where recapture rates are estimated and the assumption that all birds have the same recapture probability can be tested. Furthermore, it allows us to test whether the proportion of transients is different in fat and in lean birds (Pradel *et al.* 1997) and to gain a more reliable estimate of stopover duration than obtained by the minimum stopover duration method (Schaub *et al.* 2001).

During the course of the Swiss Ornithological Institute's project on bird migration across the Sahara in Mauritania, Palearctic passerine migrants were mist-netted at the coast and at various inland sites during spring and autumn 2003. In spring 2004 only inland sites were studied, because trapping success was negligible at the coast in spring 2003. Mist-netting took place at various sites covering most of the presumed migration period. The aims of this study were to investigate the relationship between fuel stores and stopover duration of several migrant

Figure 1. Localities mentioned in the text.

passerine species, and in particular: (1) to estimate how long migrants stop over in oases in the desert and along the coast, (2) to test whether stopover duration depended on the fat load at first capture, (3) to test whether recapture probabilities depended on individual fat loads and (4) to test whether transients were more frequent among fat than among lean birds.

STUDY SITES AND METHODS

Study sites

Between February 2003 and May 2004 various mist-netting sites were operated in Mauritania during autumn and spring migration from several days to 2.5 months. At one coastal and two inland sites (Fig. 1) the numbers of mist-netted Palearctic migrants and consecutive recaptures were high enough to address our questions using capture–recapture models. These sites were:

PK **28** (coast): this coastal site (17°43′N, 16°02′W) was situated approximately 40 km south of Mauritania's capital Nouakchott near a fishing village. Mist-nets were set up in the dunes behind the beach mainly between *Tamarix senegalensis* bushes. The nets were operated from 19 August to 25 October 2003.

Ouadâne: the oasis of Ouadâne (20°56′N, 11°35′W) is surrounded by sand desert in the southeast and rocky plateaux in the northwest. Mist-nets were set up approximately 5 km northeast of the village of Ouadâne along a dry riverbed between *Acacia raddiana*, *Balanites aegyptiaca* and *Maerua crassifolia* trees. Mist-nets were operated during spring migration from

5 March to 14 May 2003 and from 7 March to 8 May 2004. Additionally, during autumn migration the nets were operated between 23 August and 24 October 2003 but numbers of mist-netted birds and recaptures were too low for the estimation of stopover durations. Akmakam: the oasis of Akmakam (21°12′N, 11°53 W) is situated at the base of a rocky escarpment. Mist-nets were placed next to a small natural open waterbody alongside reeds *Phragmites australis* and between *Acacia raddiana* and *Balanites aegyptiaca* trees in the vicinity of the water. Additionally, birds were mist-netted in a funnel trap constructed around an acacia tree. The site was operated from 7 March to 8 May 2003.

Data collection

Birds were captured with standard mist-nets (length 6 m, height 2 m, mesh width 16 mm). The majority of the nets were placed between trees with the lower shelf reaching ground level. In addition, some nets at Ouadâne were raised up to a top height of 4–6 m. Mist-nets were in general operated daily in the morning hours from 06:00 to 11:00 h, and again from about 16:30 to 19:00 h. The time was held constant on each site throughout a season but varied between sites. The number of nets in Ouadâne was increased in spring 2004 (28) compared with spring 2003 (19) to increase the number of captures. As the study area covered by nets was not enlarged, but only the density of nets within the area increased, stopover estimates from the two years could still be compared. On some days nets were not opened or operated only for a short time due to sand storms or rain. The recapture probabilities were fixed to zero at these days in the analyses to ensure sound estimates of stopover duration. Nets were checked regularly at 30-min intervals. Captured Palearctic migrants were ringed and the amount of visible subcutaneous fat deposits was estimated following Kaiser (1993). The two former subspecies of 'Olivaceous Warbler' *Hippolais pallida* (*H. p. opaca*, *H. p. reiseri*) were treated as separate species, Western Olivaceous Warbler *H. opaca* and Eastern Olivaceous Warbler *H. p. reiseri*, respectively (Helbig & Seibold 1999, Svensson 2001, Ottosson *et al.* 2005), but only the latter was analysed. The scientific names of all species analysed are given in Table 1.

Table 1. Numbers of birds, numbers and proportions of recaptures, and fat scores at first capture of birds mist-netted at various sites in Mauritania.

Species	*n*	*n* recaptures (%)	Fat score (*n*)			
			0/1	2/3	4/5	6/7
Coast, autumn 2003						
Nightingale *Luscinia megarhynchos*	346	6 (1.7)	227	94	25	–
Reed Warbler *Acrocephalus scirpaceus*	203	11 (5.4)	56	67	77	3
Garden Warbler *Sylvia borin*	203	6 (3.0)	123	47	32	1
Pied Flycatcher *Ficedula hypoleuca*	356	9 (2.5)	213	120	23	–
Akmakam, spring 2003						
Yellow Wagtail *Motacilla flava*	58	10 (17.2)	26	22	8	2
Reed Warbler	69	7 (10.1)	10	11	17	31
Willow Warbler *Phylloscopus trochilus*	109	12 (11.0)	28	57	22	2
Orphean Warbler *Sylvia hortensis*	149	28 (18.8)	6	58	60	25
Common Whitethroat *Sylvia communis*	70	12 (17.1)	11	35	20	4
Subalpine Warbler *Sylvia cantillans*	107	13 (12.1)	7	37	45	18
Woodchat Shrike *Lanius senator*	26	5 (19.2)	4	19	3	–
Ouadâne, spring 2003						
Woodchat Shrike	25	7 (28.0)	5	19	1	–
Ouadâne, spring 2004						
Eastern Olivaceous Warbler *Hippolais pallida*	80	9 (11.3)	22	40	18	–
Ouadâne, spring 2003 and 2004						
Orphean Warbler	253	29 (11.5)	55	122	69	7
Common Whitethroat	167	16 (9.6)	12	45	78	32
Subalpine Warbler	506	53 (10.5)	29	169	205	103

Data analysis

For the estimation of stopover duration we followed the methods described in Schaub *et al.* (2001). Briefly, the stopover duration of birds present on a certain day at the stopover site is composed of two parts: the time the birds have spent at the site from arrival until the current day, and the time the birds will spend after the current day until departure. As birds cannot usually be captured every day during their presence, capture–recapture models have to be used to extract this information. Cormack–Jolly Seber models (Lebreton *et al.* 1992) allow the estimation of the local survival rate (ϕ_i), i.e. the probability that a bird present on day i at the site survived and did not emigrate from the site until day $i + 1$. Assuming that true daily survival of birds at stopover sites is 1, ϕ estimates the probability that a bird stays at the stopover site until the next day, from which the expected time until departure can be estimated (Schaub *et al.* 2001). Reverse-time capture–recapture models (Pradel 1996) are suited to estimate the seniority probability (γ_i), which is the probability that a bird present on day i has already been present at the site at day $i - 1$. γ can be used to estimate the duration of stay since arrival (Schaub *et al.* 2001). In both analytical steps, the probability of catching a bird that is present on day i (p_i), is estimated simultaneously. All the parameters might vary according to environmental and/or individual factors. To obtain robust estimates of stopover duration therefore requires three steps: (1) modelling of ϕ, (2) modelling of γ and (3) estimation of stopover duration from consideration of the previous results.

Previous analyses of ringing data from Mauritania have shown that ϕ, γ and p are best modelled to be constant across time (Heuman 2004, our unpubl. data) and show no seasonal trend (our unpubl. data). Moreover, it has been found that models that account for transients are superior for some species (Heuman 2004). A transient is an individual that was first captured at occasion i and has an emigration probability of 1 from capture occasion i to $i + 1$ (Pradel *et al.* 1997). The occurrence of transients can be modelled by implementing an age-dependent structure in the local survival rates (Pradel *et al.* 1997). Using such a model the probability that a newly captured individual is a transient (τ_i, named transient probability hereafter) can be estimated as $\tau_i = 1 - \phi_i^* \phi_i^{-1}$, where ϕ_i^* is the estimated local survival probability during the interval immediately following initial capture and ϕ_i is the estimated local survival

probability thereafter (i.e. the local survival probability of the non-transients). However, the power of the model to detect transients is low when applied to sparse datasets (Pradel *et al.* 1997). Therefore, the failure to detect transients might be due to the low number of recaptures in some species, whereas transients are certainly present when detected by the model.

We tested whether visible subcutaneous fat stores at the first capture occasion had an influence on immigration, emigration and recapture probability, and on the occurrence of transients. The emigration probability (ε) is the probability that a bird that is present at time t has left the site by time $t + 1$, and is calculated as $\varepsilon = 1 - \phi$. According to Bairlein (1985) and Biebach *et al.* (1986) we would expect that the emigration probability and the transient probability are higher in fat birds than in lean birds. We pooled the original fat scores 0–1, 2–3, 4–5 and 6–7 from the nine-level scale (Kaiser 1993, score 8 never found) to obtain four different new fat scores 0/1–6/7. Each individual was assigned to one of the four groups when it was initially captured. The most complex model considered a different transient probability for each fat score, a different emigration probability for the non-transients and a different recapture probability. Following Lebreton *et al.* (1992) we denote this model ε (trans f), p(f), where trans denotes the transient effect, and f the fat score effect. In Ouadâne, where mist-nets were operated during two spring seasons, 2003 and 2004, at the same site, we assessed in addition whether stopover behaviour differed between years. The most global model for the datasets sampled at Ouadâne was ε (trans f y), p(f y), where y denoted a year effect. We used these models to test the goodness-of-fit using 100 runs from the parametric bootstrap implemented in program MARK (White & Burnham 1999). The immigration probability (ι) is the probability that an individual has arrived at the stopover site between time t and $t + 1$, and is calculated from the seniority probability as $\iota = 1 - \gamma$. For modelling immigration we used the same model structures as for emigration probabilities. We then fitted several further models that either consider no transient-, no fat score- and/or no year-effect on emigration, immigration and recapture probabilities. We use the small sample size-adjusted Akaike's information criterion (AIC_c) to rank the models according to their support by the data (Burnham & Anderson 1998). We also calculated the AIC_c weights to assess the probability that a given model is the best among all candidate models (Burnham & Anderson 1998). Because the AIC_c

weights are probabilities, we can sum them for models that contain the variable of interest (e.g. fat or transients) on emigration, immigration or recapture probability. This sum is the probability that this variable is in the best model, and thus can be used to address our aims 2–4. Parameter estimation and modelling were conducted with program MARK (White & Burnham 1999).

For estimation of the mean and the standard error of stopover duration of the non-transients we used the non-parametric bootstrap approach implemented in program SODA (Schaub *et al.* 2001). We estimated stopover duration by using the ε, ι and p model structures with the highest AIC_c weights. For models where only one parameter (ε, ι or *p*) was dependent on fat score, the precision of stopover duration could not be estimated, because SODA does not support these models. In these cases we only estimated the mean of the stopover duration using the formulas given in Schaub *et al.* (2001).

RESULTS

At the coast the probability that a transient effect was apparent was high (> 0.7) in two out of four species (Table 2, Appendix 1). Based on the most parsimonious model, the probability that a newly caught individual was a transient ranged from 77% in Reed Warblers to 90% in Pied Flycatchers (Table 3), and was not related to fat score (Appendix 1). The probability that the best model contains no effect of fat score on emigration and immigration probability was higher than 0.74 in all species (Table 2, Appendices 1 & 2). Hence, the decision to leave this stopover site was independent of the birds' fat stores at their first capture and birds captured with high fat scores had not been longer at the site compared with birds that were caught lean. The effect of the fat score on the recapture probability was ambiguous in the Reed Warbler and the Nightingale, whereas in the Garden Warbler and the Pied Flycatcher the probability that fat had an impact was low (Table 2, Appendix 1). As expected, recapture rates in models that included fat score were higher for individuals with fat score 0/1 compared with individuals with a larger amount of fat (i.e. Nightingale: recapture probability fat score 0/1: 0.50 ± 0.25, recapture probability fat scores > 0/1: close to 0). Stopover duration of non-transient individuals calculated from the most parsimonious models varied between 1.9 days (Garden Warbler) and 4.6 days

Table 2. Probability that a specific factor (trans: transients, f: fat, y: year) is in the best structure describing emigration (ε) and recapture (*p*) in the emigration model, as well as the best structure describing immigration (ι) and recapture (p) in the immigration model. These probabilities are calculated as the sum of the AIC_c weights over all models containing a specific factor (Appendices 1–4).

Species/site	Emigration model					Immigration model				
	ε(trans)	ε(f)	ε(y)	*p*(f)	*p*(y)	ι(trans)	ι(f)	ι(y)	*p*(f)	*p*(y)
Coast, autumn 2003										
Reed Warbler	0.631	0.074	–	0.499	–	0.532	0.087	–	0.496	–
Nightingale	0.789	0.163	–	0.560	–	0.870	0.134	–	0.572	–
Garden Warbler	0.212	0.257	–	0.349	–	0.225	0.246	–	0.341	–
Pied Flycatcher	0.928	0.066	–	0.116	–	0.880	0.114	–	0.114	–
Akmakam, spring 2003										
Yellow Wagtail	0.574	0.201	–	0.371	–	0.668	0.132	–	0.424	–
Reed Warbler	0.383	0.631	–	0.405	–	0.370	0.666	–	0.287	–
Willow Warbler	0.221	0.274	–	0.098	–	0.271	0.220	–	0.089	–
Orphean Warbler	0.470	0.402	–	0.233	–	0.262	0.203	–	0.183	–
Common Whitethroat	0.512	0.026	–	0.931	–	0.285	0.034	–	0.941	–
Subalpine Warbler	0.251	0.071	–	0.048	–	0.251	0.113	–	0.050	–
Woodchat Shrike	0.201	0.206	–	0.254	–	0.192	0.187	–	0.228	–
Ouadâne, spring 2003										
Woodchat Shrike	0.260	0.074	–	0.099	–	0.244	0.085	–	0.123	–
Eastern Olivaceous Warbler	0.230	0.069	–	0.087	–	0.241	0.059	–	0.039	–
Ouadâne, spring 2003/2004										
Orphean Warbler	0.155	0.073	0.212	0.081	0.246	0.284	0.061	0.255	0.085	0.308
Common Whitethroat	0.654	0.159	0.270	0.712	0.168	0.432	0.106	0.253	0.874	0.089
Subalpine Warbler	0.784	0.404	0.278	0.346	0.426	0.830	0.426	0.286	0.354	0.444

	Transients (%)	Stopover duration (days)	se	95% CI
Coast, autumn 2003				
Nightingale	89 ± 19.6	2.4*	–	–
Reed Warbler	77 ± 11.5	4.6	1.0	2.7–6.8
Garden Warbler	0	1.9	1.3	0.1–4.0
Pied Flycatcher	90 ± 6.2	4.1	1.5	1.3–7.3
Akmakam, spring 2003				
Yellow Wagtail	85 ± 12.6	20.6	9.5	7.8–41.4
Reed Warbler	0	8.7, 23.6, 4.1, 0*	–	–
Willow Warbler	0	7.4	1.9	3.9–11.6
Orphean Warbler	38 ± 17.7	30.2	25.9	16.5–80.7
Common Whitethroat	0	17.6*	–	–
Subalpine Warbler	0	8.6	2.6	4.1–14.5
Woodchat Shrike	0	3.6	2.0	0.8–7.7
Ouadâne, spring 2003				
Woodchat Shrike	0	7.0	2.9	1.8–13.5
Ouadâne, spring 2004				
Eastern Olivaceous Warbler	0	13.8	3.6	7.4–21.8
Ouadâne, spring 2003/04				
Orphean Warbler	0	9.6	2.8	5.0–16.5
Common Whitethroat	58 ± 16.2	8.5*	–	–
Subalpine Warbler	53 ± 11.5	12.5	3.4	7.6–20.5

Table 3. Estimated probability (± se) that a newly caught individual is a transient (≈ proportion of transients), stopover duration, se and 95% CI of stopover duration of various bird species at different sites in Mauritania.

*The standard error could not be estimated, as the emigration probability or the recapture probability was fat-score dependent. In the Reed Warbler in Akmakam emigration probability was fat dependent and therefore estimates of stopover duration are given for the four fat scores separately.

(Reed Warbler) and was generally low compared with values for the inland sites in spring (Table 3).

At the inland oasis at Akmakam the probability that transients occurred was low (< 0.4) in four out of seven species, and about 0.5 in the remaining three species, reflecting uncertainty about this effect in these species (Table 2, Appendix 1). As at the coastal site, the transient probability was not related to fat scores (Appendix 1). The probability that the best model did not contain a fat effect on the emigration and immigration probability was high (> 0.7) in most species, meaning that fat score at first capture had no impact on the decision to leave the stopover site and was no indicator of how long birds had already been at the stopover site (Table 2, Appendices 1 & 2). In Orphean Warbler the impact of fat on emigration was ambiguous, thus only in the Reed Warbler did emigration and immigration probabilities clearly depend on the fat score. Individuals with fat scores 0/1 and 2/3 had the lowest emigration probabilities (0.174 ± 0.11 and 0.065 ± 0.05, respectively) and individuals with higher fat scores had the highest emigration probability (close to 1).

Stopover duration was longest at 23.6 days for Reed Warblers caught with fat score 2/3 and shorter for leaner and fatter birds. No Reed Warblers with fat score 6/7 were retrapped. The probability that fat scores affected recapture probabilities was low in all species but the Common Whitethroat, for which capture probability was low (0.02) for fat classes 2/3 and 4/5 but 0.12 and 0.22 for fat classes 0/1 and 6/7, respectively. Mean stopover duration of non-transient individuals of other species varied between 3.4 days (Woodchat Shrike) and 30.2 days (Orphean Warbler) (Table 3).

At the inland oasis Ouadâne the probability that the variable year is in the best model was low for immigration, emigration or recapture probabilities in three species mist-netted in higher numbers in both years (Table 2, Appendices 3 & 4). Therefore, the data for the two years were pooled for Orphean Warbler, Common Whitethroat and Subalpine Warbler. For Woodchat Shrike sufficient data were available only for 2003 and for Eastern Olivaceous Warbler only for 2004. The probability that the best model contains transients was low (< 0.3) in three

species, high in Subalpine Warblers (0.784) and intermediate (0.654) in Common Whitethroats (Table 2). Compared with values for the coastal site the proportion of transients was low (Table 3). In four out of five species the fat score had no impact on the transient, emigration and immigration probabilities (< 0.2); in the Subalpine Warbler it remained ambiguous whether fat was important for emigration and immigration (Table 2, Appendices 1–4). The probability that the best model contains fat scores on recapture probability was low (≤ 0.7) in all species but the Common Whitethroat. Based on the most parsimonious model recapture probability of Common Whitethroats with fat score 6/7 was much lower (close to zero) than that of individuals with a low (0/1: 0.25 ± 0.10) or medium fat score (2/3: 0.11 ± 0.06, 4/5: 0.08 ± 0.04) at first capture. Mean stopover duration of non-transient individuals varied from 7.0 days (Woodchat Shrike) to 13.8 days (Eastern Olivaceous Warbler) (Table 3).

DISCUSSION

Individuals of different species of Palearctic migrants stayed for a considerable time in oases during spring migration. Most birds were in good condition, and they were actively foraging throughout the day (Almasi 2003). This supports the conclusion of Bairlein (1985) and Biebach *et al.* (1986, 2000) that migrants in oases are not 'fall-outs', as suggested by Moreau (1972). Using capture–recapture models taking recapture probability into account, we found that the emigration and immigration probabilities do not depend on the fat stores at first capture in most species. Moreover, where transients were detected, fat birds were not more likely to be transients (i.e. to leave the stopover site the following day) than lean birds. Hence, we cannot support the conclusion of Bairlein (1985), Biebach *et al.* (1986) and Gannes (2002) that only lean individuals stay for a longer time in oases for refuelling whereas fat birds resume migration after a rest of 1 day. We also showed that stopover behaviour at the coastal stopover site in autumn was different from stopover behaviour at the two inland oases in spring.

Stopover duration in spring of many species in the western Sahara Desert was longer than stopover duration of various species on the Sinai peninsula in the eastern Sahara, even when considering that stopover duration was analysed with methods resulting in lower estimates than ours. There, stopover duration ranged from 1.5 to 3.8 days (only stopover duration

after capture, Lavee *et al.* 1991) or was 4 days for Blackcaps *Sylvia atricapilla* (minimum stopover duration, Gannes 2002). Birds that arrive early on their breeding grounds attain higher fitness because they can occupy better territories than late arriving individuals (von Haartman 1968, Alatalo *et al.* 1985, Slagsvold 1985, Møller 1994, Wiggins *et al.* 1994, Kokko 1999, Smith & Moore 2003). Birds on spring migration should therefore be under selective pressure to minimize time spent on migration (Lavee & Safriel 1989, Weber & Houston 1997, Weber *et al.* 1998). While stopping over, birds have to decide whether to depart after a short time and thereby minimize time spent at stopover sites, or to depart after a longer stay and thereby minimize the risk of not having enough fuel for the next flight step. In contrast to birds crossing the Sinai peninsula, birds stopping over in Ouadâne or Akmakam have most of the desert crossing still ahead. The optimal solution of the trade-off may be shifted towards longer stopover under such conditions, and might be an explanation for the differences of stopover duration. Although current models about decision-making for stopover duration often take the conflict between minimizing time for stopover and migration with a high fuel load into account (Alerstam & Lindström 1990, Weber *et al.* 1994, Erni *et al.* 2002), there are, to our knowledge, no studies that investigate the trade-off between the risk of migrating with low fuel supply against the fitness gain of early arrival on the breeding grounds.

Stopover duration of migrants at the coast in autumn was much shorter than in the oases in spring and the proportions of transients (77–90%) in three out of four species were also higher. In some other species, high numbers of birds were mist-netted but the numbers of recaptures were insufficient for capture–recapture analyses (e.g. Melodious Warbler *Hippolais polyglotta*: 200, 2 recaptures; Willow Warbler: 241, one recapture), which also suggests high proportions of transients. We consider that the low number of retraps and the high proportion of transients reflects the continuous flux of migration along the coast, where large areas are covered with equally suitable scattered vegetation.

In spite of the fact that habitat is a candidate explanation of the differences in the proportion of transients and stopover duration between the coastal site in autumn and the inland oases in spring, they may also be due to seasonal or regional effects. Hardly any migrants were mist-netted at a northern Mauritanian coastal site near Iouk in spring 2003,

indicating that spring migration may to a greater extent pass inland. By contrast, captures in Ouadâne in autumn 2003 with the same trapping effort as in spring were sparse. The low proportion of birds stopping over at the coast might be due to the more or less continuous availability of suitable vegetation along the coast south of Nouakchott. Longer stopover periods for intensive refuelling, as in the oases in autumn, may not be necessary because the desert has already been crossed.

Generally, emigration and immigration probabilities were independent of fat scores, suggesting that fuel stores at first capture were not important for departure decisions. Other factors like weather or fuel deposition rate could also be relevant for departure decisions (Jenni & Schaub 2003, Schaub *et al.* 2004). However, we did not include these factors in this study because we considered fuel load to be the most important factor and because we wished to keep our study comparable with former investigations dealing with the question of the role of fuel load for departure decisions. Moreover, the probability of becoming a transient was independent of fat scores. This is in contrast to the conclusion that birds captured in lean condition at stopover sites rest for a longer period to refuel than fat birds (Cherry 1982, Biebach 1985, Biebach *et al.* 1986, Loria & Moore 1990, Bairlein 1992, Yong & Moore 1997, Gannes 2002; but see Safriel & Lavee 1988, Kuenzi *et al.* 1991). This conclusion was based on the assumption that recapture probability is independent of fat scores and that birds not recaptured had resumed migration. However, at stopover sites fat birds are known to be less active during the day than lean birds (Bairlein 1985, Yong & Moore 1993, Titov 1999) and may be more risk-sensitive and behave more secretively (Moore & Simm 1986), which can result in low recapture probabilities of fat birds (Bibby *et al.* 1976, Titov 1999), as shown in this study for the Nightingale at the coast and the Common Whitethroat inland.

The different results of our study compared with Bairlein (1985) and Biebach *et al.* (1986) could also be due to the different season of the analyses. It was shown experimentally that fat birds in autumn show more migratory restlessness in the night than lean birds, both in the field (Bairlein 1985) and under laboratory conditions (Biebach 1985, Bairlein 1987; but see examples in Bairlein & Gwinner 1994, Korner-Nievergelt *et al.* 2002). Our results from the inland oases were from spring, and it is possible that the migration strategy in spring is different from that in autumn, when different cues for the departure decision may be used.

Lindström and Alerstam (1992) argued that constant stopover duration, independent of fuel load, would be disastrous if birds resume migration to cross an ecological barrier simply when told to do so by an internal clock. Although this is reasonable on autumn migration where selective pressure may act mainly on successful termination of migration, the situation may be different in spring when there is also a selective pressure for early arrival in the breeding grounds. With respect to the above-mentioned trade-off between early arrival on the breeding grounds and migration with high fuel loads, birds might risk a dangerous crossing before it is too late for successful breeding. Therefore, and especially for small, short-lived passerines, an all-or-nothing decision-making process may control their departure.

There are some shortcomings in our approach, however, with respect to the correlation of departure decision with fuel stores. First, we do not know whether birds arriving with different fat stores stay for different times at the stopover site. This cannot be inferred from our analysis because we only recorded the fat stores at first capture, which might not be identical with the fat stores on arrival. Secondly, if departure decision is based on fuel load, fat stores at take off might also not be identical with fat stores at capture. Multistate models could be applied to investigate this question (Schaub, 2006) but our data were too sparse for such an analysis. Nevertheless, our data do indicate that the decision-making process to resume migration across the desert with hardly any additional stopover sites further north is not governed by a fuel threshold (Gannes 2002) and birds may leave the oases without substantial fat loads. A similar situation was found during spring migration near Lake Chad where the median minimum stopover duration did not differ between birds which gained body mass and those showing mass loss (Ottosson *et al.* 2002). Additionally, Safriel and Lavee (1988) found that the initial weight did not always determine stopover length of migrants.

We have shown that birds stopping over in oases in spring may rest for a considerable time, which is not dependent on fat score at first capture, and that a smaller proportion of resting migrants are transients than was formerly suggested. It still remains to be determined, however, what proportion of birds use oases as stopover sites for refuelling compared with birds that rest in the desert without refuelling or even perform a non-stop flight. The answer is crucial

to a full understanding of migration strategies across ecological barriers such as the Sahara and for optimal bird migration theories in general.

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Appendix 1. ΔAIC$_c$ (difference of AIC$_c$ between current and the best model) and AIC$_c$ weights of the eight emigration models fitted to the capture–recapture data and the significance probability of the bootstrap goodness-of-fit test (*P*) of the model ε (trans f), *p*(f) for various species mist-netted in Mauritania. ε denotes the local emigration probability, *p* the recapture probability, trans refers to a transient effect, f to a fat score effect, and (.) to constancy. Bold type: the most parsimonious model.

Model	ε(trans f),*p*(f)		ε(trans),*p*(f)		ε(f),*p*(f)		ε(.),*p*(f)		ε(trans f),*p*(.)		ε(trans),*p*(.)		ε(f),*p*(.)		ε(.),*p*(.)		*P*
	ΔAIC$_c$	AIC$_c$	ΔAIC$_c$	AIC$_c$	ΔAIC$_c$	AIC$_c$	ΔAIC$_c$	AIC$_c$	ΔAIC$_c$	AIC$_c$	ΔAIC$_c$	AIC$_c$	ΔAIC$_c$	AIC$_c$	ΔAIC$_c$	AIC$_c$	
Coast, autumn 2003																	
Reed Warbler	11.590	0.001	0.290	0.286	7.219	0.009	0.975	0.203	6.429	0.013	**0.000**	**0.331**	3.757	0.051	2.295	0.105	0.57
Nightingale	8.352	0.007	**0.000**	**0.454**	7.404	0.011	3.276	0.088	4.152	0.057	1.031	0.271	3.276	0.088	5.873	0.024	0.12
Garden Warbler	15.408	< 0.001	2.226	0.096	6.790	0.010	0.363	0.243	8.717	0.004	1.902	0.113	0.363	0.243	**0.000**	**0.292**	0.22
Pied Flycatcher	12.511	0.002	4.083	0.102	11.881	0.002	8.717	0.010	6.135	0.037	**0.000**	**0.787**	6.865	0.025	6.238	0.035	0.48
Akmakam, spring 2003																	
Yellow Wagtail	15.605	< 0.001	1.488	0.182	8.201	0.006	1.473	0.183	7.435	0.009	**0.000**	**0.383**	1.456	0.185	4.047	0.051	0.55
Reed Warbler	9.863	0.004	1.009	0.326	5.416	0.036	5.250	0.039	4.751	0.050	10.136	0.003	**0.000**	**0.541**	18.658	< 0.001	0.73
Willow Warbler	15.958	< 0.001	5.867	0.024	6.837	0.015	4.091	0.059	8.698	0.006	1.731	0.191	1.162	0.253	**0.000**	**0.453**	0.26
Orphean Warbler	4.949	0.025	5.452	0.020	1.132	0.170	5.673	0.018	1.731	0.126	**0.000**	**0.299**	2.607	0.081	0.275	0.261	0.46
Common Whitethroat	12.353	0.001	0.055	0.450	6.587	0.017	**0.000**	**0.463**	10.010	0.003	4.162	0.058	9.077	0.005	9.874	0.003	0.52
Subalpine Warbler	16.912	< 0.001	8.387	0.010	8.546	0.009	6.246	0.029	11.319	0.002	2.003	0.239	4.770	0.060	**0.000**	**0.651**	0.49
Woodchat Shrike	18.028	< 0.001	4.153	0.050	7.324	0.010	1.445	0.194	10.512	0.002	1.983	0.149	1.445	0.194	**0.000**	**0.400**	0.36
Ouadâne, spring 2003																	
Woodchat Shrike	20.268	< 0.001	6.509	0.023	10.009	0.004	4.248	0.072	9.712	0.005	1.899	0.232	4.447	0.065	**0.000**	**0.600**	0.34
Ouadâne, spring 2004																	
E. Olivaceous Warbler	18.889	< 0.001	8.790	0.008	9.253	0.006	4.306	0.073	12.639	0.001	2.090	0.221	4.643	0.062	**0.000**	**0.629**	0.48

Appendix 2. ΔAIC_c (difference of AIC_c between current and the best model) and AIC_c weights of the eight immigration models fitted to the capture–recapture data for various species mist-netted in Mauritania. ι denotes the local immigration probability, p the recapture probability, trans refers to a transient effect, f to a fat score effect, and (.) to constancy. Bold type: the most parsimonious model.

Model	ι(trans f),p(f)		ι(trans),p(f)		ι(f),p(f)		ι(.),p(f)		ι(trans f),p(.)		ι(trans),p(.)		ι(f),p(.)		ι(.),p(.)	
	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c
Coast, autumn 2003																
Reed Warbler	11.878	0.001	0.380	0.235	6.512	0.011	0.266	0.249	6.480	0.011	**0.000**	**0.285**	2.991	0.064	1.360	0.144
Nightingale	8.355	0.008	**0.000**	**0.500**	8.503	0.007	4.374	0.056	4.153	0.062	1.08	0.300	4.374	0.056	6.991	0.015
Garden Warbler	15.401	< 0.001	2.213	0.099	6.933	0.009	0.504	0.233	8.707	0.004	1.802	0.122	0.504	0.233	**0.000**	**0.300**
Pied Flycatcher	12.415	0.002	4.018	0.100	11.689	0.002	8.557	0.010	6.036	0.036	**0.000**	**0.742**	4.605	0.074	6.194	0.034
Akmakam, spring 2003																
Yellow Wagtail	14.684	< 0.001	1.130	0.236	8.691	0.005	1.643	0.183	4.467	0.016	**0.000**	**0.416**	2.635	0.111	5.115	0.032
Reed Warbler	11.079	0.002	1.862	0.225	6.534	0.022	5.393	0.038	4.128	0.072	4.170	0.071	**0.000**	**0.570**	16.311	< 0.001
Willow Warbler	16.348	< 0.001	6.365	0.021	7.426	0.012	4.430	0.056	9.165	0.005	1.972	0.191	1.844	0.203	**0.000**	**0.511**
Orphean Warbler	10.010	0.003	6.875	0.016	2.756	0.129	5.351	0.035	7.881	0.010	1.572	0.233	4.252	0.061	**0.000**	**0.512**
Common Whitethroat	15.266	< 0.001	1.998	0.246	6.320	0.028	**0.000**	**0.667**	12.844	0.001	5.738	0.038	9.695	0.005	7.724	0.014
Subalpine Warbler	16.095	< 0.001	8.289	0.010	7.637	0.014	6.298	0.026	10.245	0.004	1.907	0.237	3.736	0.095	**0.000**	**0.615**
Woodchat Shrike	18.534	< 0.001	4.659	0.043	7.733	0.009	1.855	0.176	11.018	0.002	2.217	0.147	1.855	0.176	**0.000**	**0.446**
Ouadâne, spring 2003																
Woodchat Shrike	20.033	< 0.001	6.335	0.025	6.731	0.020	4.055	0.078	12.663	0.001	2.000	0.218	4.451	0.064	**0.000**	**0.593**
Ouadâne, spring 2004																
E. Olivaceous Warbler	19.130	< 0.001	8.860	0.008	9.578	0.006	6.558	0.025	12.638	0.001	2.143	0.232	5.121	0.052	**0.000**	**0.676**

Appendix 3. ΔAIC_c (difference of AIC_c between current and the best model) and AIC_c weights of the 32 emigration models fitted to the capture–recapture data and the significance probability of the bootstrap goodness-of-fit test (P) of the model ε (trans y f), p(y f) for three species for which data from spring 2003 and spring 2004 from Ouadâne were pooled. ε denotes the local emigration probability, p the recapture probability, trans refers to a transient effect, y to a season effect, f to a fat score effect, and (.) to constancy. Bold type: most parsimonious model.

Model	Orphean Warbler ΔAIC_c	Orphean Warbler AIC_c	Common Whitethroat ΔAIC_c	Common Whitethroat AIC_c	Subalpine Warbler ΔAIC_c	Subalpine Warbler AIC_c
ε(trans y f),p(y f)	38.695	< 0.001	30.080	< 0.001	16.723	< 0.001
ε(trans y f),p(f)	30.097	< 0.001	21.927	< 0.001	11.713	0.001
ε(trans y f),p(y)	25.177	< 0.001	17.591	< 0.001	7.709	0.004
ε(trans y f),p(.)	23.550	< 0.001	15.373	< 0.001	6.303	0.009
ε(y f),p(y f)	23.672	< 0.001	17.190	< 0.001	9.122	0.002
ε(y f),p(f)	17.859	< 0.001	8.293	0.005	3.739	0.031
ε(y f),p(y)	13.487	< 0.001	6.005	0.015	4.675	0.019
ε(y f),p(.)	11.379	0.001	3.776	0.044	2.634	0.054
ε(f),p(y f)	16.315	< 0.001	11.421	0.001	3.591	0.033
ε(f),p(f)	10.034	0.002	7.902	0.006	6.749	0.007
ε(f),p(y)	5.788	0.018	5.840	0.016	9.474	0.002
ε(f),p(.)	3.729	0.051	5.176	0.022	7.515	0.005
ε(trans y),p(y f)	16.015	< 0.001	8.300	0.005	2.201	0.066
ε(trans y),p(f)	9.822	0.002	1.582	0.133	6.803	0.007
ε(trans y),p(y)	7.574	0.007	5.175	0.022	3.971	0.027
ε(trans y),p(.)	5.523	0.021	3.260	0.057	3.191	0.041
ε(trans f),p(y f)	24.229	< 0.001	17.492	< 0.001	3.212	0.040
ε(trans f),p(f)	17.849	< 0.001	10.151	0.002	5.423	0.013
ε(trans f),p(y)	13.621	< 0.001	6.282	0.013	2.835	0.048
ε(trans f),p(.)	11.495	0.001	4.228	0.035	0.765	0.136
ε(y),p(y f)	12.387	0.001	6.841	0.010	7.079	0.006
ε(y),p(f)	6.228	0.015	2.666	0.077	9.979	0.001
ε(y),p(y)	4.026	0.044	12.562	0.001	8.649	0.003
ε(y),p(.)	1.994	0.121	11.395	0.001	6.621	0.007
ε(trans),p(y f)	11.822	0.001	4.425	0.032	1.822	0.080
ε(trans),p(f)	5.764	0.018	**0.000**	**0.293**	3.277	0.039
ε(trans),p(y)	3.615	0.054	4.906	0.025	2.024	0.073
ε(trans),p(.)	1.558	0.151	4.157	0.037	**0.000**	**0.200**
ε(.),p(y f)	10.284	0.002	4.768	0.027	5.087	0.016
ε(.),p(f)	4.228	0.040	1.761	0.121	7.948	0.004
ε(.),p(y)	2.042	0.119	10.896	0.001	6.646	0.007
ε(.),p(.)	**0.000**	**0.329**	12.703	0.001	4.658	0.019
P		0.35		0.40		0.48

Appendix 4. ΔAIC_c (difference of AIC_c between current and the best model) and AIC_c weights of the 32 immigration models fitted to the capture-recapture data for three species for which data from spring 2003 and spring 2004 from Ouadâne were pooled. ι denotes the local immigration probability, *p* the recapture probability, trans refers to a transient effect, y to a season effect, f to a fat score effect, and (.) to constancy. Bold: most parsimonious model.

	Species					
	Orphean Warbler		Common Whitethroat		Subalpine Warbler	
Model	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c
ι(trans y f),*p*(y f)	38.143	< 0.001	31.606	< 0.001	15.480	< 0.001
ι(trans y f),*p*(f)	29.595	< 0.001	24.396	< 0.001	10.943	0.001
ι(trans y f),*p*(y)	25.064	< 0.001	19.862	< 0.001	7.701	0.004
ι(trans y f),*p*(.)	23.063	< 0.001	18.161	< 0.001	6.516	0.007
ι(y f),*p*(y f)	13.441	< 0.001	17.462	< 0.001	8.789	0.002
ι(y f),*p*(f)	15.724	< 0.001	8.551	0.005	3.143	0.038
ι(y f),*p*(y)	11.430	0.001	7.476	0.008	6.025	0.009
ι(y f),*p*(.)	9.285	0.003	5.282	0.023	3.965	0.025
ι(f),*p*(y f)	12.264	0.001	11.872	0.001	2.887	0.043
ι(f),*p*(f)	10.208	0.002	6.382	0.013	6.187	0.008
ι(f),*p*(y)	5.686	0.016	6.973	0.010	10.221	0.001
ι(f),*p*(.)	4.013	0.037	5.180	0.025	8.332	0.003
ι(trans y),*p*(y f)	11.746	0.001	9.539	0.003	2.002	0.066
ι(trans y),*p*(f)	9.363	0.003	3.206	0.066	5.898	0.009
ι(trans y),*p*(y)	6.644	0.010	7.981	0.006	2.487	0.052
ι(trans y),*p*(.)	4.672	0.026	6.579	0.012	2.266	0.058
ι(trans f),*p*(y f)	20.135	< 0.001	19.522	< 0.001	2.132	0.062
ι(trans f),*p*(f)	17.994	< 0.001	11.791	0.001	4.293	0.021
ι(trans f),*p*(y)	13.246	< 0.001	8.423	0.005	2.292	0.057
ι(trans f),*p*(.)	11.547	0.001	6.196	0.015	0.442	0.145
ι(y),*p*(y f)	8.455	0.004	7.361	0.008	8.284	0.003
ι(y),*p*(f)	5.979	0.014	1.985	0.121	9.895	0.001
ι(y),*p*(y)	3.331	0.052	13.698	< 0.001	8.326	0.003
ι(y),*p*(.)	1.333	0.141	12.145	0.001	6.298	0.008
ι(trans),*p*(y f)	7.564	0.006	6.185	0.015	2.475	0.052
ι(trans),*p*(f)	5.746	0.015	0.247	0.289	3.531	0.039
ι(trans),*p*(y)	2.645	0.073	7.775	0.007	1.742	0.076
ι(trans),*p*(.)	1.222	0.149	6.267	0.014	**0.000**	**0.181**
ι(.),*p*(y f)	6.458	0.011	5.156	0.025	6.373	0.007
ι(.),*p*(f)	4.532	0.028	**0.000**	**0.327**	8.604	0.002
ι(.),*p*(y)	1.439	0.133	11.744	0.001	6.564	0.007
ι(.),*p*(.)	**0.000**	**0.274**	11.576	0.001	4.794	0.016