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Songbird migration across the Sahara: the non-stop hypothesis rejected!

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Billions of songbirds breeding in the Western Palaearctic cross the largest desert of the world, the Sahara, twice a year. While crossing Europe, the vast majority use an intermittent flight strategy, i.e. fly at night and rest or feed during the day. However, it was long assumed that they overcome the Sahara in a 40 h non-stop flight. In this study, we observed bird migration with radar in the plain sand desert of the Western Sahara (Mauritania) during autumn and spring migration and revealed a clear prevalence of intermittent migration. Massive departures of songbirds just after sunset independent of site and season suggests strongly that songbirds spent the day in the plain desert. Thus, most songbirds cross the Sahara predominately by the intermittent flight strategy. Autumn migration took place mainly at low altitudes with high temperatures, its density decreased abruptly before sunrise, followed by very little daytime migration. Migration was highly restricted to night-time and matched perfectly the intermittent flight strategy. However, in spring, when migratory flights occurred at much higher altitudes than in autumn, in cool air, about 17% of the songbird migration occurred during the day. This suggests that flying in high temperatures and turbulent air, as is the case in autumn, may lead to an increase in water and/or energy loss and may prevent songbirds from prolonged flights into the day.

Keywords: bird migration; desert crossing; non-stop migration; passerine; water stress

1. INTRODUCTION

The Palaearctic–African bird migration system comprises nearly four billion songbirds (Moreau 1972). Most songbirds carrying out such long-distance movements migrate only nocturnally in Europe (Dorka 1966; Winkler 1989; Bruderer & Liechti 1999) as well as in the semi-desert of Israel (Bruderer 1994; Bruderer & Liechti 1995). Flight costs of flapping flyers are expected to be lower in laminar air layers at night than in turbulent air during the day (Kerlinger & Moore 1989). Additionally, daytime can be used to recover (Schwilch *et al.* 2002; Fuchs *et al.* 2006) and restore energy and water reserves. When crossing the Sahara, they encounter harsh environmental conditions over a distance of about 2000 km. To cope with heat and scarcity of food and water, they store fat and protein in anticipation (Fry *et al.* 1970; Piersma 1990; Biebach 1998; Jenni & Jenni-Eiermann 1998; Klaassen *et al.* 2000). Therefore, it was long hypothesized that songbirds should cross the Sahara by a long non-stop flight and not waste water and energy by resting during the day in the hot and dry sand desert (Moreau 1961; see also Biebach 1990). Birds occasionally observed in the desert were considered as fallouts. However, the few songbirds captured in the desert were in good body condition and continued their migration after sunset, suggesting an intermittent flight strategy in at least some species or individuals (Bairlein 1985; Biebach *et al.* 1986; Bairlein 1988). Since the temporal and spatial patterns of songbird migration across the desert were never quantified, the question of how many songbirds overcome the Sahara by an intermittent or a non-stop flight of 40 h remained unanswered. Migration models (Carmi *et al.* 1992; Klaassen 1995) and wind tunnel experiments (Engel 2005) revealed some evidence that due to the extreme environmental conditions songbirds flight time might be restricted by water consumption.

We quantified for the first time, to our knowledge, spring and autumn songbird passage in the Western Sahara, Mauritania, by carrying out extensive radar studies at an oasis and two additional sites surrounded by at least 300 km of nearly vegetationless desert. According to the non-stop hypothesis, songbirds, which find themselves after a nocturnal flight at sunrise over the open desert, should continue their flight across the desert. However, songbirds having not yet reached the open desert until dawn are supposed to land before sunrise, as they do in Europe and Israel (Bruderer 1994; Bruderer & Liechti 1995, 1999). Thus, recording non-stop migration at a given site in the desert, we would not expect a continuous flow of migrants throughout the day, but a limited passage of birds for a time period corresponding to the length of a night. Considering non-stop migration, we expected a wave of songbird migrants passing our study sites, timed in relation to the distance to the southern or northern edge of the desert, i.e. the Sahel savannah and the Atlas Mountains, respectively. Assuming that the departure from these last refuelling areas occurred at dusk, which is a general pattern for migrants in North America, Europe and Israel (Gauthreaux 1971; Hebrard 1971; Alerstam 1990; Bruderer 1994; Bruderer & Liechti 1995, 1999; Åkesson *et al.* 1996; Moore & Aborn 1996; Bolshakov & Chernetsov 2004), we calculated for each radar site and season an expected period of passage, based on the averaged measured ground speeds (50 km h^{-1}, see §2). Thus, according to the non-stop hypothesis, the temporal pattern of the passage should differ between the sites according to their different distances from the

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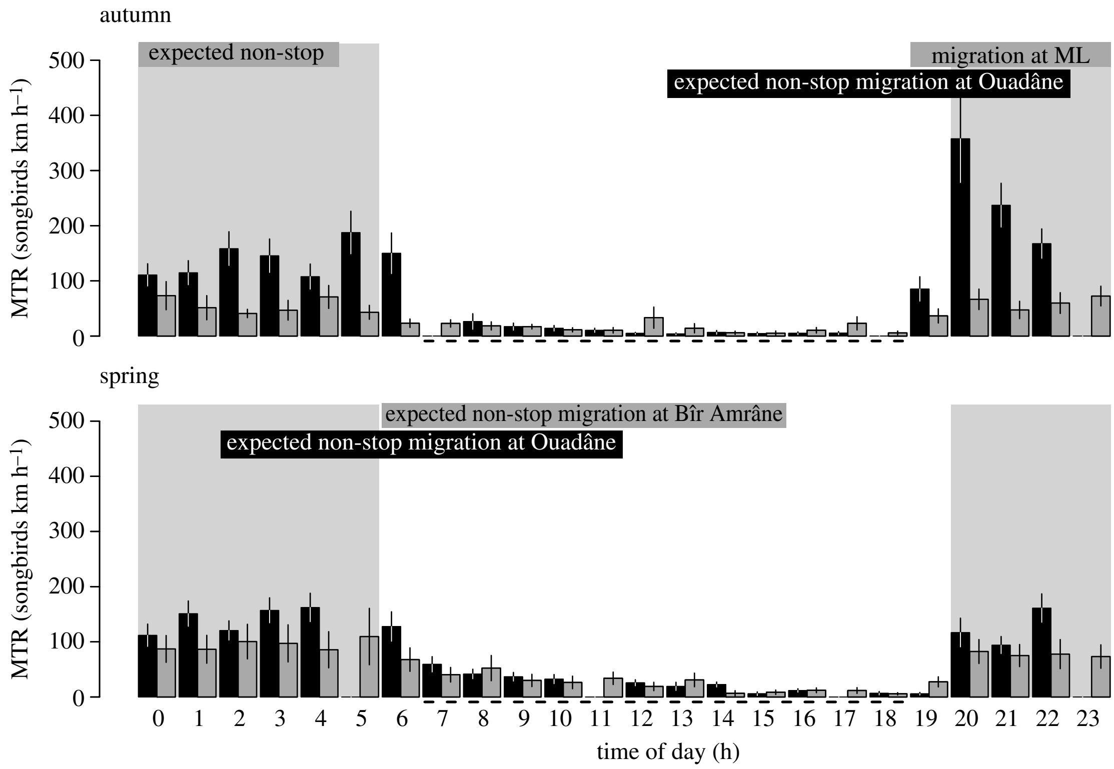

Figure 1. Migration traffic rate (MTR) of songbirds (mean ± s.e.) in the course of the day in autumn and spring, at the constant site Ouadâne (oasis, $n_{\text{autumn}} = 63$ days, $n_{\text{spring}} = 57$ days; black bars) and two temporal sites (grey bars) in the plain sand desert, Mohammed Lemna (ML) in autumn ($n = 12$ days) and Bîr Amrâne in spring ($n = 23$ days). The shaded area marks the measurements considered for the nocturnal migration and the dashed line (below *x*-axis) those for diurnal migration. The horizontal bars indicate the time periods at which the hypothetical non-stop waves of songbirds are supposed to fly over the study sites. The times are calculated based on the distances to the next major departure sites (the Atlas Mountains and Sahel Savannah) and an average ground speed of 50 km h^{-1} (cf. figure 2). Missing bars at Ouadâne are due to lacking measurements.

departure sites, while the intermittent hypothesis would lead to an identical pattern at all sites, with take-off at dusk and landing at dawn (figure 1).

2. MATERIAL AND METHODS

Data were collected in Mauritania close to the oasis Ouadâne, located about 500 km east of the Atlantic coast (20°56′ N, 11°35′ W), in autumn (24 August–25 October 2003) and spring (15 March–10 May 2004), and at two sites (Mohammed Lemna, 18°35′ N, 08°38′ W; Bîr Amrâne, 22°47′ N, 08°43′ W) 300 km further east in the plain sand desert in autumn (19–30 September 2003) and in spring (03–25 April 2004), respectively (figure 2).

To quantify bird migration, a fixed beam method similar to the one suggested by Bruderer (1971) was used, but with a fully computerized recording system. At Ouadâne, fixed beam measurements were carried out at a low and high elevation angle (11° and 79°) every hour and at the other two sites at three different elevation angles three times per hour (Mohammed Lemna, 8°, 28° and 79°; Bîr Amrâne, 6°, 28°, 79°). In doing so, high and low altitudes were surveyed with nearly the same effort. The resulting number of fixed beam measurements for autumn was 2680 in Ouadâne and 2064 at Mohammed Lemna; for spring, it was 2050 in Ouadâne and 3971 at Bîr Amrâne. The beam was directed towards the west (270°) and thus perpendicular to the main migration direction (Schmaljohann *et al.* in press). South of the Ouadâne site was a small vegetation strip within the sandy desert, whereas to the north the rocky desert extended for several hundred kilometres. Therefore, only spring departure data might be directly influenced by the oasis close by. The two desert sites were separated from the next oasis by several hundred kilometres of plain sand desert. The recording time was 4 min and the detection range for songbirds was restricted to about 7 km (Schmaljohann, unpublished data). This system collection of the echo signature of each target crossing the beam and distinguished between birds and insects on the basis of their echo signatures. This identification was essential as insect echoes made up a substantial proportion of all echoes. To quantify songbird passage, we selected only songbirds out of all the detected birds according to their echo signature, i.e. wing beat pattern (Bruderer 1969). Swallows and corvids differ in migration strategy (being diurnal migrants) and flight type (resulting in special wing beat patterns) from the majority of passerines, i.e. Motacillidae, Turdidae, Sylvidae and others, and were excluded from the samples accordingly. For further information about the use of radar for ornithological purposes see Bruderer (1997). Songbirds migrating in the desert during the day may be either nocturnal migrants prolonging their flights or diurnal migrants; in the Sahara, the daytime migration consisted mainly of diurnally migrating nocturnal migrants (Schmaljohann *et al.* in press).

To estimate the time the songbirds would need to cover the distance from the major departure areas to the study sites, we determined their average ground speed at Ouadâne. Single songbirds were tracked by radar and their ground speeds were recorded. Average ground speed was 15.3 ± 5.0 m s^{-1} ($n_{\text{autumn+spring}} = 6485$), which we simplified to 50 km h^{-1}.

The night was defined to last from 20.00 to 05.00 and day from 07.00 to 18.00, because civil twilight occurred during the sixth and the nineteenth hour of the day throughout all the

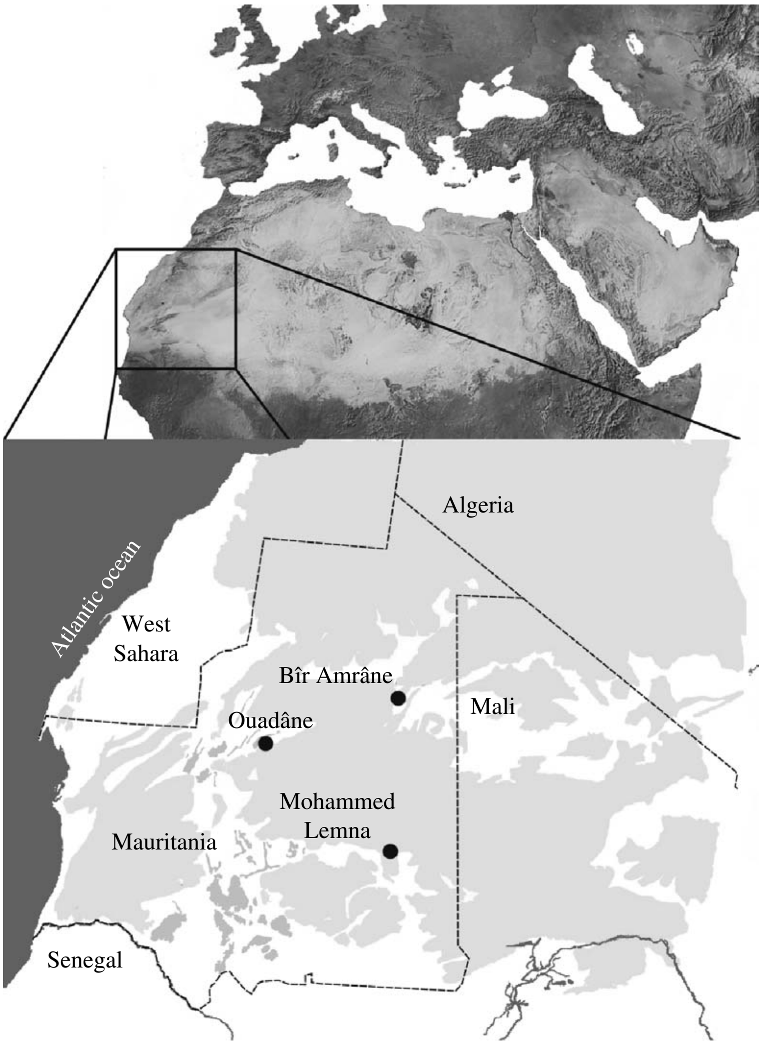

Figure 2. Location of the study sites in Mauritania. The upper map provides an overview of the Sahara with the general location of the studied areas (rectangle), expanded below. In the lower graph, the three study sites are given, whereas the oasis of Ouadâne is situated at the transition from the sandy desert to a stony plateau, Bîr Amrâne and Mohammed Lemna are within the plain sand desert.

study periods. Statistics were calculated using the statistical software package R (R Development Core Team 2005).

3. RESULTS

At all sites, songbird migration intensity increased immediately after sunset, remained relatively high during the night and decreased smoothly after sunrise in spring but abruptly in autumn, especially at the oasis (figure 1). The proportion of diurnal migration (figure 1) at the oasis was significantly lower in autumn (5%) than in spring (17%; Mann–Whitney test, two-tailed, $n_{\text{autumn}}=62$ days, $n_{\text{spring}}=55$ days, $W=2401$, $p<0.0001$). In both seasons and at all sites, migration intensity was very low during the afternoons (from 13.00 to 20.00; Ouadâne autumn, 1.6%; Ouadâne spring, 7.7%; Mohammed Lemna autumn, 6.2%; Bîr Amrâne spring, 4.7%).

4. DISCUSSION

In spring, the last major stopover site before the desert crossing is the Sahel savannah. Any bird taking-off from there and flying non-stop would reach Ouadâne at the earliest at 02.00. The last birds of such a non-stop wave would pass the oasis at around 11.00. This hypothetical non-stop wave would then reach the desert site (Bîr Amrâne), about 200 km further north, 4 h later (average songbird ground speed was about 50 km h^{-1}; figure 2). In autumn, major departure areas are within the Atlas Mountains. First songbirds taking-off there would be expected to reach Ouadâne around midday, and last birds of the non-stop wave should have passed the oasis by 22.00. Owing to the more southern and more inland location of Mohammed Lemna (about 270 km), we assumed that the hypothetical non-stop wave would fly over this site from 19.00 to 04.00. Apparently, the diurnal pattern of songbird migration did not match these expected patterns of the non-stop hypotheses. The massive departure of songbirds after sunset and the persistent migration through the night, independent of site and season, indicate clearly that take-off took place in the vicinity of the study sites and, thus, songbirds rested in the desert during the day (figures 1 and 2). Therefore, the data give strong evidence that intermittent migration is the predominate strategy of songbirds to cross at least the Western Sahara. This confirms the suggestion of Bairlein (1985, 1988), Biebach *et al.* (1986) and Biebach (1990), who concluded from capturing data that at least some songbirds cross the desert intermittently. Taking the four billion songbirds crossing the Sahara in autumn (Moreau 1972) and distributing them evenly in time (90 days) and space (11 000 000 km^2), we would expect to find each day about four birds per kilometre squared. At Mohammed Lemna, a line transect count (1500 m) in the sand desert with a few tiny bushes was carried out daily in the mornings during the study period. At three out of ten transect counts a single subalpine warbler (*Sylvia cantillans*) was observed. When the few small bushes in an area of 200 $\times$ 20 m at Bîr Amrâne were searched intensively for birds on 13 out of 19 days, passerine migrants were found; the average number was 5 ± 4 (s.d.) songbirds and the most common species were willow warbler (*Phylloscopus trochilus*, $n=19$), common whitethroat (*Sylvia communis*, $n=18$) and melodious warbler (*Hippolais polyglotta*, $n=12$). Thus, passerines were encountered regularly in the Sahara, although finding them remained hard.

In contrast to autumn, when migration was highly restricted to night-time, passerines prolonged their migratory flights far into the day in spring (figure 1.), but the amount varied extremely from day to day. There is strong evidence from preliminary work, analysing data from Ouadâne 2003 (Schmaljohann *et al.* in press), that this occasional daytime migration, consisting mainly of nocturnal migrants continuing their migration, occurred only under good tailwind conditions. We therefore conclude that passerines prolong their migratory flights opportunistically, depending on the wind conditions during the morning. A slight proportion of songbirds extended migration into the day also at Mohammed Lemna during autumn, where, according to the non-stop hypothesis, no migration should occur before 19.00 (figure 1). Therefore, prolongation of migratory flights into the day seems to be a common pattern in songbirds crossing the Sahara, probably influenced strongly by actual environmental conditions (see below and Schmaljohann *et al.* in press). Such prolongations were also observed in garden warblers (*Sylvia borin*) when crossing the Mediterranean Sea (Grattarola *et al.* 1999) and in other nocturnal migrants when crossing the open sea (Williams & Williams 1978; Spina & Pilastro 1999; for reviews, see Gauthreaux 1978 and Martin 1990). Nevertheless, if the daytime passage in spring was formed by a common wave of non-stop migration, we would expect a time lag between the wave at Ouadâne and Bîr Amrâne of about 4 h. However, there is no evidence for such a difference between the sites, and daytime migration was not recorded everyday. Thus, there is no strong support for non-stop migration, but we cannot fully rule out that some passerines might migrate non-stop.

Although we could point out that most passerines do not cross the Sahara in a non-stop flight, most of them do so in the sense of nutritional terms. Passerines resting in the open desert still migrate ‘non-stop’, because they do not feed during the daytime stopovers. Thus, for passerines, it still remains necessary to intensively refuel before crossing such barriers, as shown, e.g., in northern Africa by Odum (1963) and Bairlein (1988). Hence, our findings are in line with the notion that land birds achieve a maximum departure fuel load just before barrier crossings (Marsh 1983; Dierschke *et al.* 2005).

What might be the reasons that nocturnal migrants prolong their flight into the day regularly in spring, but rarely in autumn? Wind tunnel experiments have shown that under desert conditions flying birds have a negative water budget (reviewed by Kvist 2001; Engel 2005). Red knots (*Calidris canutus*) showed a net water loss with temperatures higher than 20°C (Kvist 2001), whereas flying rose-coloured starlings (*Sturnus roseus*) always possessed a net water loss independent of ambient temperature (Engel 2005). Moreover, flight time was limited by high temperatures (27°C) to 4.5 h in European starlings (*Sturnus vulgaris*; Engel 2005). Nevertheless, temperature did not markedly influence the selection of flight altitudes by nocturnal migrants (Liechti *et al.* 2000; Liechti 2006). Accordingly, in spring, passerine migration in this study was mainly concentrated within the anti-trades (tailwinds for spring migrants) at a height of 2–4 km above ground level. The cool (around 10°C) and relative humid (about 40%) air may result in a relatively low water loss (Carmi *et al.* 1992). In autumn, most birds flew below 1 km above ground level in the trade wind zone (tailwinds for autumn migrants), where temperatures are high (25–35°C) and humidity is low (about 30%; our unpublished data). Hence, water loss is expected to be much higher in autumn than in spring. We therefore assume that spring migrants flying at high altitudes occasionally prolong flight into the day (Schmaljohann *et al.* in press), while autumn migrants flying at low altitudes are restrained by the high diurnal flight costs (water and/or energy). Similarly, water loss might be responsible for the difference in nocturnal flight activity between spring and autumn in the Negev desert (Bruderer & Liechti 1995). In the Negev, migrants did not prolong their flight into the day either in spring or in autumn, but in spring nocturnal flight activity lasted for the whole night, while in autumn it ceased early during the second half of the night.

In general, flight duration of songbirds under desert conditions might be limited either due to the excessive water loss by flying in the blazing sun and through hot and dry air or due to the excessive energy loss by flying in turbulent air during the day instead of in laminar air flow at night (Kerlinger & Moore 1989; Carmi *et al.* 1992; Engel 2005). Therefore, resting on the ground would reduce expenditure of water and/or energy compared with flying with extra costs in daytime. We suggest that the relative advantages of nocturnal flights prevent most songbirds from performing non-stop flights across the Sahara.

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